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THE GENUS *PROTEMNODON* OWEN (MARSUPIALIA: MACROPODIDAE) IN THE UPPER CAINOZOIC DEPOSITS OF QUEENSLAND

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ABSTRACT

The genus *Protemnodon* Owen, 1874, is re-defined on the basis of extensive collections in the Queensland Museum, derived largely from the Upper Cainozoic fluviatile deposits of the Darling Downs area, southeastern Queensland. Five species of this extinct macropodid genus are recognized, three of which, *P. anak*, *P. brehus* and *P. roechus* are found to be restricted to Pleistocene sediments. Two new species, *P. chinchillaensis* and *P. devisi*, are described from the Late Pliocene Chinchilla Sand in the western Darling Downs and of these, *P. chinchillaensis* is at present known only from that Formation. *P. devisi* is shown to be present also in unnamed sediments near Mullaley, New South Wales. It is morphologically very similar and probably closely related to *P. otibandus*, described from the Middle Pliocene Otibanda Formation in New Guinea and reported from the Lower Pliocene marine Jemmy's Point Formation in Victoria. Both new species are shown to represent major elements in the Chinchilla fauna.

Samples in all species defined are sufficiently large to enable statistical evaluation of most of the cheek teeth to be undertaken and results are generally in keeping with what has been recorded for other fossil and living macropodid populations.

Remains of macropodids comprise a major part of the collections of fossil marsupials derived from the Upper Cainozoic deposits of Queensland, and among these, the genus *Protemnodon* Owen, 1874, is particularly well represented. By far the majority of specimens referable to this genus in the holdings of the Queensland Museum have been derived from the classical Darling Downs deposits in southeastern Queensland. These form the basis for the present study.

The presence of fossil marsupials was noted in the Darling Downs area shortly after the first settlement of the area in the early 1840's. Early collections appear to have been restricted to material derived from high terrace Pleistocene fluviatile deposits along the Condamine River and its major tributaries in the eastern portion of the district. Later collections also accumulated from the Chinchilla area in the western Darling Downs and for many years specimens from both these sources were ascribed a Pleistocene age. It has now been shown by Bartholomai (1972a) that an age difference exists between the deposits. The Chinchilla Sand in the west is considered to be of Late Pliocene age. The probability of this age difference existing had been originally suggested by Woods (1956)

and prior to evidence for superposition becoming available, was strongly supported by the presence between them of faunal distinctions, usually at a specific level.

A number of studies on extinct macropodids occurring in the Darling Downs deposits have already been presented (Woods, 1960; Bartholomai, 1963, 1966, 1967, 1970, 1972a, 1972b) and the present study constitutes a contribution to a better understanding of the taxonomy of the genus *Protemnodon* in the light of the large samples available and the improved knowledge of the geological history of the area. The *Protemnodon* samples, because of their size, allow a reassessment of the species represented, involving an evaluation of the teeth, and other parameters and morphological variation present. Results are of potential value in correlation of Australian continental deposits and in providing a better basis towards an understanding of the Upper Cainozoic evolutionary history of this interesting genus.

The Queensland study of *Protemnodon* is supported by a less detailed investigation of the distribution of the genus in Australia based on collections in Australian museums, and on published work. Results, particularly from the available holdings of the Australian Museum, Sydney, are of value in consideration of the eastern Australian distribution of *Protemnodon* and the geographical variation present. Exact temporal relationships of these samples are, however, difficult to determine. Specimens from the Australian Museum are prefixed throughout by AM.

All measurements throughout are in millimetres.

Genus **Protemnodon** Owen, 1874

Protemnodon Owen, 1873, p. 128 (*nomen nudum*).

Protemnodon Owen, 1874, pp. 274–5 (type species *Protemnodon anak* Owen, 1874, by subsequent designation of Simpson, 1930, and restated by Tate and Archbold, 1937, = *Macropus anak* Owen, 1859, *nomen nudum*). Palmer (1904) had previously questionably suggested *P. anak* as the type species.

Considerable confusion exists regarding the taxonomic status of the genus *Protemnodon* Owen, based on fossil material, and on the genera *Macropus* Shaw, 1790, and *Wallabia* Trouessart, 1905, based on modern species (Ride, 1962).

Stirton (1963) provides a very full discussion on previous concepts of *Protemnodon* and attempts, through an extended comparison of cranial and dental characters, to justify its separation from other macropodines. Unfortunately, his revised generic diagnosis for *Protemnodon*, includes many characters common to most macropodine genera. Stirton (1963) emphasises, however, that the separation of *Protemnodon* must depend upon utilization of all available criteria and cannot be effected by single character considerations. He concludes that the genus is separable from *Wallabia sensu lato* (Calaby, 1966) and from other macropodine genera and this contention is supported by the present study, but Stirton's limits for the genus *Wallabia* are not supported by either recent or fossil taxonomic considerations (Bartholomai, 1972a). Previously, Raven (1929), followed by many subsequent authorities, had considered *Wallabia* and *Protemnodon* synonymous, although Troughton (1957) reiterated their generic distinctness but presented little evidence to support this conclusion. Stirton (1963) has evaluated some

of the characters used by Tate (1948) who supported their synonymy and has indicated the extreme difficulty of defining generic limits, a result of the marked convergence in the evolution of the subfamily as a whole (Bartholomai, 1972a).

The confusion initiated by Owen (1877) regarding the association of upper teeth of *Protemnodon* with the named mandibular remains, and the association of upper and lower dentigenous fragments of the genus *Sthenurus* Owen, 1874, has also been outlined by Stirton (1963). Owen's misidentifications have been shown to have resulted from the misconception that the genera were closely related, and were aided by the sequence of discovery of the various remains.

No doubt currently exists regarding the correct association of fragments in *Protemnodon,* although much confusion remains regarding the identity and number of species present and the correct association of upper and lower jaw fragments within these.

Owen (1874) described four species of *Protemnodon* from the Queensland Pleistocene fluviatile deposits. These he named *P. anak, P. og, P. roechus* and *P. mimas.* In the same publication, Owen (1874) also described *Sthenurus brehus* (= *P. brehus*) from the Pleistocene cave earth deposits at Wellington Caves, New South Wales. An additional Pleistocene species, *P. antaeus* was later described by Owen (1877) from the fluviatile deposits of the eastern Darling Downs. All species were based on mandibular remains, with the exception of *P. brehus.*

Lydekker (1887) reduced the number of species recognized to three, *P. anak, P. brehus* and *P. roechus,* but referred them to the genus *Macropus.* The number was again reduced by De Vis (1895) and only one species, *P. anak,* was recognized at that time. De Vis employed the generic name *Halmaturus* Illiger, 1811, a junior secondary homonym of *Macropus,* for the species. Since that time there have been several suggestions that the variation exhibited in the Upper Cainozoic protemnodonts would justify the recognition of a larger number of species. Stirton (1963) states that even if only late Pleistocene fossils occur in the Darling Downs, it is not unreasonable that two species could be represented. He indicates that it is extremely doubtful that there are as many as six, and still questionable that there are more than two.

Fossiliferous late Pleistocene deposits at Lake Menindee, New South Wales, have been reported by Tedford (1967) who records *P. brehus* as a moderately rare element in the fauna. It is possible that this sample represents a mixture of two large species. Cranial and post-cranial remains have been described. Tedford (1967) suggests that De Vis's (1895) concepts on the morphological limits of Owen's species were very wide, and by accepting *P. brehus* as a valid species within the *Protemnodon* group, he infers that at least two species exist in the late Pleistocene deposits.

Two species, *P. otibandus* and *P. buloloensis* have been described by Plane (1967) from the Middle Pliocene Awe Fauna of the Otibanda Formation, New Guinea. Plane (1972) has recorded *P. buloloensis* in the marine Lower Pliocene (Kalimnan) Jemmy's Point Formation in Victoria and has suggested that this species is also present in the Chinchilla fauna. *P. buloloensis* shows some morphological similarities to part of the Chinchilla Sand sample but, although close relationships are apparent, sufficient differences exist for this to be maintained as a distinct mainland Pliocene species. It is of interest to note that elements of the post-cranial skeleton are also known for *Protemnodon* in the

Awe Fauna, including the peculiarly robust, short pes, and the forearm and manus in *P. otibandus*. No attempt has been made to sort the post-cranial elements of *Protemnodon* in the Queensland Museum holdings, although it is apparent that morphologically similar elements to those described from the Otibanda Formation are present in reasonably large numbers from both the Pleistocene and Late Pliocene deposits.

The present study indicates that five species of *Protemnodon* are represented in the Upper Cainozoic deposits of the Darling Downs. No taxonomic distinctions are evident to suggest additional taxa within samples collected from elsewhere in Queensland or used for comparison from New South Wales localities. Three of the species present are derived from the Pleistocene fluviatile deposits and cave and fissure fill deposits of similar or perhaps younger age, while two species occur in the Chinchilla Sand. Nomenclature for the Pleistocene species follows that previously outlined by Lydekker (1887).

Representative histograms prepared for cheek teeth dimensions in the combined *Protemnodon* sample from the Pleistocene deposits, illustrated in Figure 1, show marked bimodality for the characters considered, and this is true for most parameters in the sample. A similar but less well-defined bimodality exists in the combined sample for the Chinchilla Sand material. Within the Pleistocene sample, the bimodality is by no means equal, there being considerably more specimens represented relating to lower values than to higher values in the characters assessed. Males and females in modern macropodine populations are represented approximately by nearly equal numbers of individuals (Kirkpatrick, pers. comm.). For this reason, the size differences which exist within the broad groups defined by the histograms suggest that these do not represent sexual dimorphism within single species. Bartholomai (1971) has shown that in the living Grey Kangaroo, *Macropus giganteus* Shaw, 1790, sexual dimorphism in the cheek teeth is a factor warranting attention but this does not manifest itself in spectacularly bimodal frequency distributions. In the same study, Bartholomai also indicates that in the large, living Sandy Wallaby, *M. agilis* (Gould, 1842), no significant sexual dimorphism is present in the sizes of the cheek teeth. In both living species mentioned, marked dimorphism does appear to exist in other characters less readily observed in fossil specimens and of these, for example, basicranial length appears to differ to a much greater extent between the sexes.

Bartholomai (1972a) suggests that the diversification of the fauna recorded from the Darling Downs deposits may reflect accumulations deposited under climatic fluctuations with attendant faunal shifts so that sympatric conditions of existence need not necessarily apply. It is inconceivable from comparison with extant species, however, that the differences in each combined Upper Cainozoic sample could represent subspecific differences within single species. Similarly, the differences within each combined sample cannot be attributed to successional subspeciation because material from both limits of a particular histogram is derived from the same stratigraphic level in single sites.

The size differences which occur in both the Pleistocene and Late Pliocene samples are regarded as being of taxonomic importance, and can be utilized in the initial sorting of collections. Together with some morphological characters, sufficient differences are available to establish the distinctness of the species here redefined and described. As an example, the individuals contributing to the larger values in the bimodal frequency

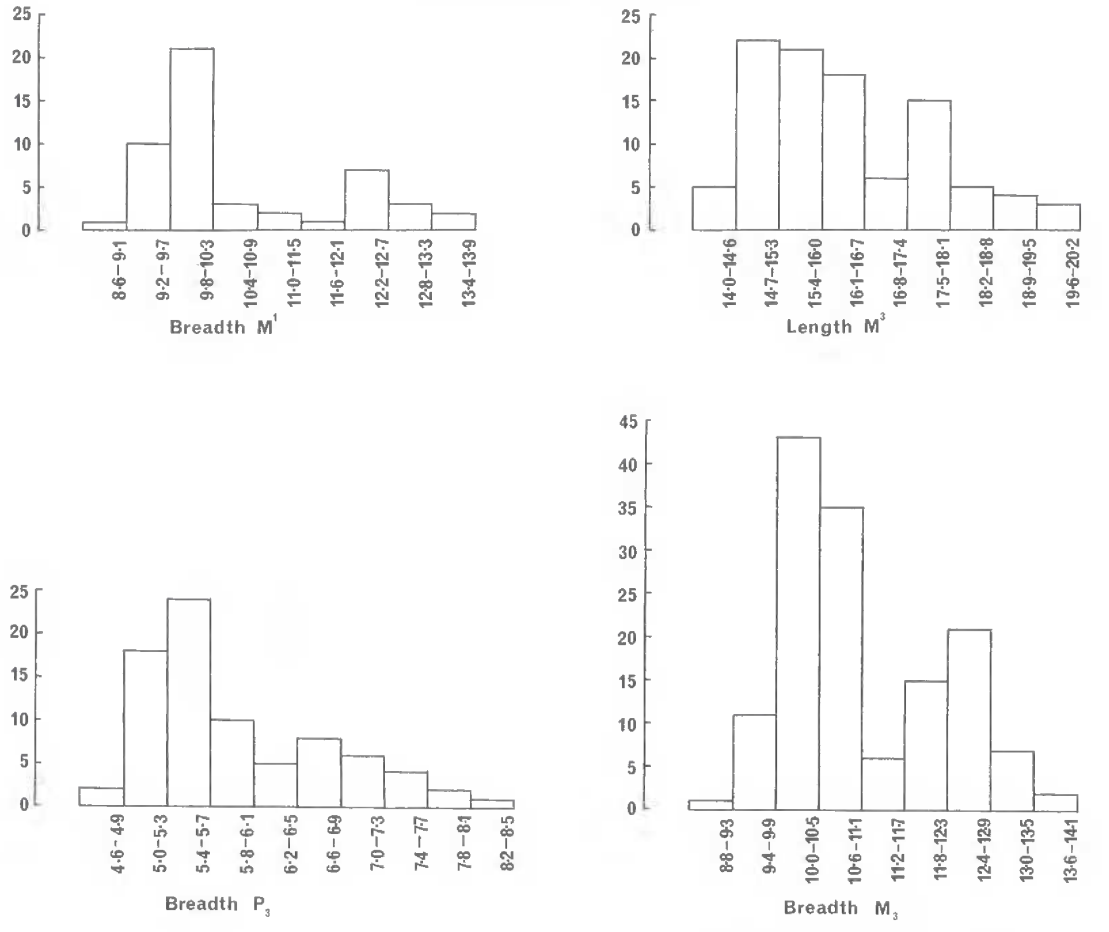

FIG. 1: Representative histograms for cheek teeth parameters in the combined *Protemnodon* samples from the Pleistocene fluviatile deposits of the eastern Darling Downs.

distributions for the Pleistocene material are further separable into two species, *P. brehus* and *P. roechus*, by structural differences, while those contributing to the smaller values differ morphologically from these, and are referable to *P. anak*. In no case, however, is complete separation of a population possible by size alone. It is obvious that, because of initial overlap of values, the statistical Coefficient of Difference would fall well below the value of 1·5 or larger, suggested by Ride (1964) to be required to define even subspecific differences. As with characters of value in defining the generic limits, it is necessary to apply as many criteria as possible in the separation of the species.

Cranial remains in all species, for the most part, are fragmentary. Fortunately exceptions to this are present, although apart from *P. anak* only one reasonably complete cranium is known in the Queensland collections. Within *P. anak* only F616, an almost

complete cranium, is present in an undistorted condition but this is adequately supported by several distorted specimens. *P. roechus* is represented by one partial cranium, F6581. A partial cranium of *P. brehus* is present in the Western Australian Museum, from Lake Tandau in the Lower Darling Region, New South Wales, but at present the Late Pliocene species lack referred complete or near complete crania. Knowledge of the cranial anatomy of these is restricted to fragmentary maxillary remains.

Stirton (1963, figs. 2–3) has illustrated partial crania, but of these only the subject of his figure 2, AM F2221, of *P. anak*, would appear to be referable with certainty to the genus. The second specimen illustrated by Stirton (1963, fig. 3), AM F16490, appears to differ markedly from crania of *P. anak* in the Queensland Museum and from the other specimen figured by Stirton (1963). The most obvious differences are seen in the posterior view, illustrated in Stirton (1963, fig. 3a), where the zygomatic processes of the squamosals are markedly convergent dorsally and nearly flattened laterally, whereas in *P. anak* these are less convergent dorsally and present a rounded lateral profile. The trend towards dorsal convergence in the cranium, AM F16490, is also seen in the occipital surface which is relatively narrower dorsally and broader ventrally, this imparting a moderate divergence to the paraoccipital processes. The cranium, F6581, here referred to *P. roechus*, does present greater dorsal convergence in posterior view than in *P. anak* and AM F16490 may relate to this or the other larger protemnodont, *P. brehus*. No cheek teeth are preserved in AM F16490 and thus some doubt remains regarding the taxonomic position of this specimen.

Stirton (1963) has attempted a reconstruction of the cranium of *Protemnodon* but has had to restore much of the dorsal outline. It is felt that the premaxillary and the upper incisors added to this reconstruction and based upon AM F37806, are referable to one of the larger species of *Protemnodon* from the Pleistocene, whereas the bulk of the recon-

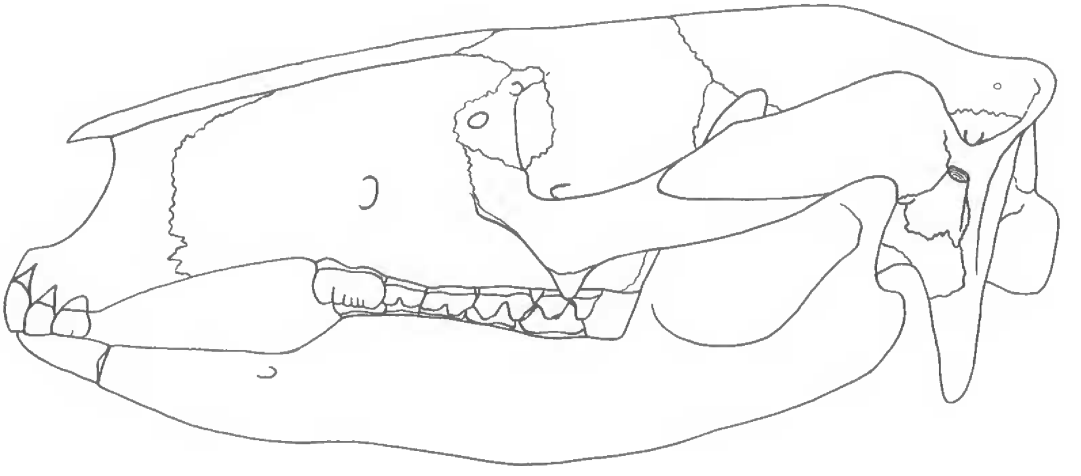

FIG. 2: Reconstruction of the cranium of *Protemnodon anak* Owen, based on the skull, F616, the premaxilla, F651, and the mandibular ramus, F617, $\times \frac{1}{2}$.

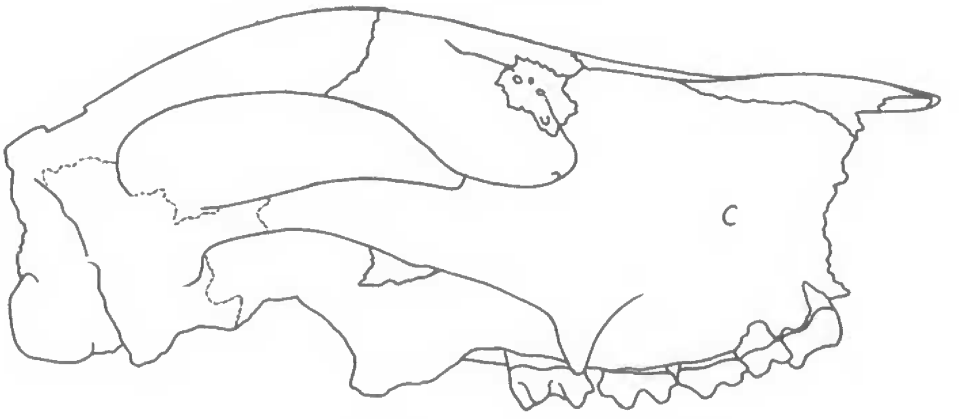

FIG. 3: Outline illustration of partial cranium, F6581, of *Protemnodon roechus* Owen, $\times\frac{1}{2}$.

struction is based on AM F2221, of *P. anak*. The reconstruction of the skull of the type species, *P. anak*, here presented in Figure 2, illustrates the much flatter nature of the dorsal surface of the cranium in that species compared with the genera *Macropus* Shaw and *Wallabia* Trouessart and with Stirton's (1963) reconstruction. An outline illustration of the cranium of *P. roechus* is presented in Figure 3, and illustrates the extent of some of the differences present between the larger and smaller Pleistocene *Protemnodon* species. The differences relate particularly to the length of the nasals but the shape of the premaxillae and the size of the upper incisors are also important. The specimen of *P. brehus* in the Western Australian Museum from Lake Tandau, although incomplete, suggests that shortening of the nasals may also be a feature of that species; this is supported by the specimen illustrated by Owen (1877, pl. 109, figs. 9–10).

Much has been written on the similarities and differences present between the crania of *Protemnodon* and other living and extinct macropodine genera (Stirton, 1963). A series of equal area grid diagrams, as proposed by Thompson (1959), have been prepared using a specimen of *Wallabia bicolor* (Desmarest, 1804), the type species of *Wallabia*, as a standard, and including specimens of *Protemnodon* and species of *Macropus* for comparison. To add some measure of control, all specimens compared are at a similar stage of dental eruption. Results are illustrated in Figure 4. These show that at least in the type species of *Protemnodon*, the cranium is more flattened, more elongate in the area of the diastema, broader across the anterior of the palate, and with the alveoli for the incisors forming a broader U-shaped pattern in occlusal view than in *W. bicolor*. The basisphenoid and presphenoid are more posteriorly positioned with respect to the posterior palatine margin. Some distortion precludes the use of the cranium of *P. roechus* in this regard, but because of restriction of the nasals, the grid distortion would indicate shortening of this area compared with both *W. bicolor* and *P. anak* and the same is also probably true of *P. brehus*.

Species of *Macropus* show great similarity in the degree of grid distortion produced and most pronounced differences relate only to relative size. Differences from *Wallabia*

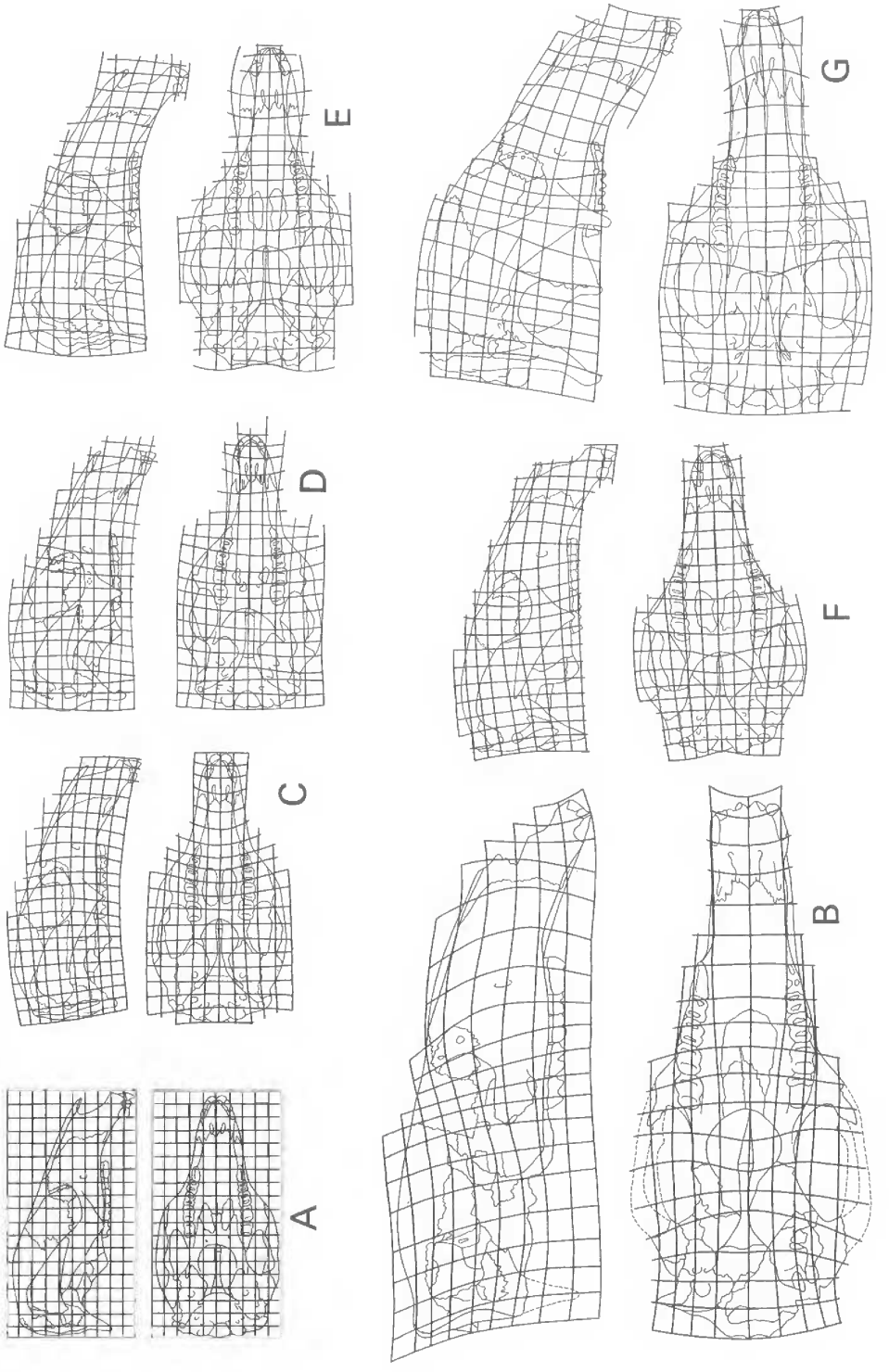

FIG. 4: Equal area grid diagrams based on A, *Wallabia bicolor* as standard, for B, *Protemnodon anak* (F616); C, *Macropus dorsalis*; D, *M. rufogrisea*; E, *M. elegans*; F, *M. agilis*; and G, *M. giganteus*.

and *Protemnodon* are considerable. The most obvious distinction lies in the much stronger declination of the rostral area of the skull, the elongation of this area, particularly anteriorly, and the shortening and broadening of the base of the cranium. Such diagrams, although representing generalizations by the nature of their preparation, are considered of value in illustrating and indicating differences in these morphologically similar genera.

Protemnodon is widespread in its distribution throughout Australia during the Pleistocene and is recorded from numerous localities in all States except the Northern Territory. Pliocene occurrences are less well represented in collections, but the genus is known from the Otibanda Formation in New Guinea, from the Chinchilla Sand in Queensland, and from the Lower Pliocene Jemmy's Point Formation (Plane, 1972) and possibly the late Pliocene Hamilton Fauna in Victoria (Turnbull and Lundelius, 1970). Earlier history of the group is not well documented although Stirton *et al.* (1967b) have recorded but not described a protemnodont from the Wipijiri Formation in the Lake Eyre Basin, South Australia. Bartholomai (1972a) has suggested that major radiation in *Protemnodon,* similar to other macropodids, probably took place in Australasia during and particularly after the Miocene.

Revised Generic Diagnosis: Cranium flattened with limited declination of rostral area, diastema elongate, and anterior of palate broad; high, thin lateroventral ovale crest separates pterygoid cavity from ovale foramen and continues onto alisphenoid bulla as posterior rim of foramen. Palatine vacuities absent. Upper incisors broadly U-shaped in occlusal view. Canine usually absent but may be present in vestigial state. P^2 elongate with high longitudinal crest and low cingulum; crest transected by two variable, vertical or near vertical sets of labial and lingual ridges with production of cuspules at crest. Posterior fossette present. DP^3 molariform, similar to upper molars. P^3 elongate with high longitudinal crest and low lingual cingulum which terminates above paracone or more anteriorly; crest transected by two to five sets of vertical or near vertical labial and lingual ridges, usually with development of cuspules at crest; hypocone prominent and posterior fossette well defined. Upper molars with forelink usually absent but strong anterior ridge from paracone to anterior cingulum usually present; median valley near planar transversely; accessory ridge from paracone to metacone usually crosses labial moiety of median valley.

Mandible with diastema long, and with well defined lateral groove extending posteriorly as far as M_3 in some species; symphysis elongate, unankylosed, varying in elevation from horizontal to about 20° to base of mandible; articular facet of condyle nearly twice as wide transversely as antero-posteriorly long. I_1 vertically deep, lanceolate, with tip strongly incurved. P_2 elongate, secant, with longitudinal crest straight or somewhat curved, and with crest transected by vertical or near vertical sets of labial and lingual ridges. DP_3 molariform, similar to lower molars; P_3 elongate, with longitudinal crest transected by one to five sets of vertical or near vertical labial and lingual ridges, with cuspules usually developed at crest; crest straight or somewhat curved. Lower molars with talonid basin narrowly U-shaped, with or without tuberculation at lingual extremity and near planar transversely; posterior cingulum may be present.

Protemnodon anak Owen, 1874

(Plates 9–12)

Macropus anak Owen, 1859, p. 185 (*nomen nudum*).
Protemnodon anak Owen, 1873, p. 128 (*nomen nudum*).
Protemnodon og Owen, 1873, p. 128 (*nomen nudum*).
Protemnodon anak Owen, 1874, pp. 275–7, pl. 25, figs. 1–4, 7–10, 11–14; 1877, pp. 428–30, pl. 85, figs. 1–4, 7–10, 11–14; Etheridge Jnr., 1892, p. 677; Raven, 1929, p. 255; Simpson, 1930, p. 76; Tate and Archbold, 1937, p. 410; Tate, 1948, p. 297; Troughton, 1957, p. 187; Stirton, 1963, p. 137, fig. 13a.
Protemnodon og Owen, 1874, pp. 277–8, pl. 25, figs. 5–6; 1877, p. 430, pl. 85, figs. 5–6; Etheridge Jnr., 1892, p. 678; Palmer, 1904, p. 883; Simpson, 1930, p. 76; Stirton, 1963, p. 139, fig. 13b.
Halmaturus anak (Owen): Krefft, 1875, p. 208; De Vis, 1895 (*partim*), pp. 104–9, pl. 17, figs. 5–10.
Sthenurus atlas Owen, 1876 (*partim*), pp. 210–2, pl. 25, fig. 2, pl. 26, fig. 4.
Macropus anak (Owen): Flower, 1884, p. 715; Lydekker, 1887, pp. 214–8; Lydekker, 1894, p. 257; Lydekker, 1896, p. 257; Palmer, 1904, p. 883.
[?]*Macropus anak* (Owen): Scott and Lord, 1924, pp. 6, 8.

MATERIAL: F3398, cast of holotype of *Protemnodon anak* Owen, British Museum (Natural History) No. M.1895, partial left mandibular ramus with P_3–M_4, adult, Darling Downs, (figd Owen, 1874, pl. 25, figs. 1–2; 1877, pl. 85, figs. 1–2).

F3396, cast of holotype of *Protemnodon og* Owen, British Museum (Natural History) No. 35963, partial left mandibular ramus with P_3–M_4, adult, Gowrie, Darling Downs, (figd Owen, 1874, pl. 25, figs. 5–6; 1877, pl. 85, figs. 5–6).

Seventy-two juvenile mandibular rami, 105 adult mandibular rami, 16 isolated lower teeth, 6 partial adult crania, 6 premaxillary remains, 19 juvenile maxillae, 71 adult maxillae and 26 isolated upper teeth from the following localities in the eastern Darling Downs: King Creek; King Creek, between Pilton and Nobby; King Creek, at Ravensthorpe, Upper Pilton; King Creek, near M.R. 039454 Clifton 1 mile map; King Creek, at M.R. 039454 Clifton 1 mile map; King Creek, at M.R. 134444 Liverpool Range 1 mile map; King Creek, at M.R. 098465 Liverpool Range 1 mile map; King Creek, at M.R. 873335 Clifton 1 mile map; King Creek, near M.R. 047452 Clifton 1 mile map; at M.R. 951360 Clifton 1 mile map; Ravensthorpe, Pilton; Clifton; Gowrie; Gowrie Creek; ? Gowrie; near Dalby; Jimbour, via Macalister; Jimbour Creek; Springvale, near St Ruth; Condamine River, 'Armour', Macalister; Macalister; Goombungee; Cambooya; Mt Leinster, Dalby, in a well at 40 feet; 'Cardoch', near Dalby, at Por. 137, Par. St Ruth; Por. 137, Par. St Ruth; Freestone Creek; and from the eastern Darling Downs (particular localities unspecified).

SPECIFIC DIAGNOSIS: Species relatively large. Mandible moderately shallow, with symphysis elongate; symphysis ascends at low angle anteriorly; lateral groove on ramus extends posteriorly well below alveolar margin to below anterior root M_2.

I_1 elongate, relatively markedly curved in occlusal view, with enamel produced into dorsolabial and ventrolingual flanges. P_2 relatively elongate, with longitudinal crest moderately high, mostly straight but curving slightly lingually anteriorly; crest transected by two or three sets of vertical labial and lingual ridges; cuspules developed. DP_3 with relatively high lophids; broad, rounded ridge descends anteriorly from metaconid to anteriorly swollen base of protolophid; anterolabial fossette present; weak ridge descends anterolabially from entoconid to talonid base, close to midlink; posterior cingulum well defined. P_3 elongate, usually slightly constricted at posterior one-third, with longitudinal crest relatively high, straight or slightly convex lingually; crest transected by three or four sets of vertical labial and lingual ridges; cuspules developed. Lower molars with high lophids; trigonid basin and anterior cingulum relatively narrow; anterolabial fossette

present; slight ridge descends from entoconid towards talonid; posterior cingulum normally present, well defined.

Upper incisors broadly U-shaped; I^1 moderately large, while I^3 elongate at distal edge. C^1 occasionally present, vestigial. P^2 relatively elongate, with crown margins converging anteriorly; longitudinal crest high, straight or slightly concave labially; crest transected by at least two sets of vertical labial and lingual ridges; cuspules present; lingual cingulum extends anteriorly to above paracone; cingulum slightly tumid in lingual view. DP^3 with high lophs, and occasionally with slight suggestion of forelink; strong, high ridge ascends anteriorly from paracone to labial limit of cingulum; posterior ridge from paracone ascends to unite across median valley with slight ridge from metaloph, partially closing off labial moiety of valley. P^3 elongate, being generally longer than M^4, with crown markedly concave labially; longitudinal crest high, markedly to slightly concave labially; crest transected by two to four sets of vertical labial and lingual ridges; cuspules present; lingual cingulum continues anteriorly to above paracone; lingual ridge from first cuspule along crest usually prominent; cingulum markedly tuberculate in lingual view. Upper molars slightly constricted across median valley, with high lophs and usually no trace of forelink; strong ridge ascends anteriorly to limit of relatively narrow anterior cingulum; strong ridge usually curves posterolingually from paracone onto labial surface of midlink; occasionally slight anterior ridge present from metacone.

Description: Mandible moderately shallow, relatively thick; base of symphysis near planar, ascending at low angle anteriorly; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit relatively shallow, at posterior symphysial limit; diastema elongate with diastemal crest posteriorly acute, more rounded anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen comparatively small, oval, close to diastemal crest about one-third distance along crest from P_3 to limit of ramus. Ramus with moderately deep lateral groove extending posteriorly to below anterior root of M_2, usually disrupted by roots of P_3; groove positioned well below alveolar margin. Diagastric process separated from base of angle by very shallow post-diagastric sulcus, bounded above by shallow diagastric fossa; this fossa separated above from shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, with shelf angle not developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of alveolar margin; masseteric foramen moderately large, with deep masseteric fossa. Angle of mandible markedly inflected, flexed posteriorly at margin, broadly rounded posteriorly, ascending at high angle to posterior flared limit of masseteric crest. Anterior margin of coronid process reclining at approximately 15° to vertical; condyle broadly rounded anteroposteriorly, near planar transversely, approximately oval in occlusal view.

I_1 elongate, deeply rooted; slightly curved in lateral view, markedly curved in occlusal view, developing subhorizontal facet of wear with upper incisors and mesial wear facet at tip by approximation with other lower incisor; root compressed, oval in section; crown subquadrantal in section, tapering and blade-like anteriorly, enamelled laterally,

this produced dorsolabially and ventrolingually into flanges; crown also enamelled ventromesially; distally, tip wears rapidly, ultimately producing broadly rounded anterior margin.

P_2 relatively elongate, approximately semi-circular to sublunate in occlusal view, with lingual surface occasionally weakly convex but usually nearly straight or slightly concave and labial surface markedly convex. Longitudinal crest secant, slightly to moderately strongly curving lingually in its posterior extension, and curving slightly lingually anteriorly; crest transected by two (50%, n = 20) or three (50%, n = 20) sets of vertical labial and lingual ridges with production of cuspules at crest; where third set developed, posterior ridges poorly defined; anterior cuspid of crest well defined, but posterior cuspid less well developed; base of crown somewhat tumid. Height of enamel frequently greater anteriorly than posteriorly.

DP_3 molariform, subtriangular in basal outline, unconstricted or slightly constricted across talonid basin, with lophids moderately high, slightly convex posteriorly. Hypolophid much broader than protolophid. Trigonid basin moderately narrow, its length being less than distance between lophids. Forelink moderately high, strong, curving anterolingually from protoconid to near mid-point of relatively low anterior cingulum, slightly labiad to axis of crown; broad, rounded ridge descends anteriorly from metaconid to anteriorly swollen base of protolopid in lingual moiety of trigonid, occasionally produced as ridge to lingual portion of anterior cingulum; labially, anterior cingulum unites with base of protolophid with production of anterolabial fossette; lingual moiety of trigonid pocket-like, near planar, but labial moiety descends at high angle into fossette. Midlink moderately high, strong, curving anterolingually from hypoconid across talonid basin to unite with short, posterior ridge from near midpoint of protolophid; weak ridge descending anterolabially from entoconid passes into talonid basin close to midlink, occasionally continuing across talonid to below metaconid; slight ridge usually descends posteriorly from metaconid into talonid; talonid basin sharply U-shaped, near planar, descending only slightly labially and lingually from midlink. Posterior cingulum well defined, ascending slightly lingually, with slight ridge ascending towards entoconid from extremity. Infrequently, cingulum extends only partially across posterior of hypolophid. Base of crown occasionally tumid, particularly at labial extremity of talonid.

P_3 elongate, robust, deeply rooted; crown subovate in basal outline but usually slightly constricted at posterior one-third; labial margin slightly convex, with lingual margin occasionally convex but usually near straight or rarely concave. Longitudinal crest secant, straight or slightly convex lingually, rarely slightly sinuous between anterior and posterior cuspids, slightly curving lingually in its posterior extension; crest transected by three (50%, n = 38) or four (50%, n = 38) major sets of vertical labial and lingual ridges with production of cuspules at crest; where fourth set developed, posterior ridges generally poorly defined; occasionally with small intermediary ridges developed at crest; anterior cuspid of crest well defined, but posterior cuspid less well developed; base of crown somewhat tumid. Height of enamel usually similar anteriorly and posteriorly.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline slightly constricted across talonid basin; lophids high, slightly convex posteriorly, with hypolophid broader than protolophid in M_1, approximately equal in M_2 and M_3, and generally considerably

narrower in M_4. Trigonid basin relatively narrow, rarely broader, its length approximately equalling distance between lophids. Forelink moderately high, strong, curving anterolingually from protoconid to near midpoint of low, relatively narrow, anterior cingulum slightly labiad to axis of crown; slight ridges descend anteriorly from metaconid towards trigonid, and posteriorly towards talonid basin; anterior surface of protolophid in lingual moiety of trigonid usually swollen; anterior cingulum usually descends at high angle from forelink, uniting with protolophid base, frequently defining anterolabial fossette; cingulum somewhat expanded anterolingually, but abruptly truncated; lingual moiety of trigonid near planar, but labial moiety descends at moderate to relatively high angle. Midlink moderately high, strong, curving anterolingually from hypoconid to unite with slight ridge from near mid-point of protolophid above talonid; slight ridge descends anterolabially from entoconid towards talonid; occasional slight ridges descend posterior surface of protolophid; talonid basin sharply U-shaped, near planar, descending only slightly labially and lingually from midlink. Posterior cingulum normally present, usually well defined, occasionally tumid, ascending lingually, frequently with slight ridge ascending towards entoconid from lingual extremity. Base of crown somewhat tumid, especially at labial extremity of talonid basin.

Cranium large, length being 289·8–290·3 (n = 2) in adult specimens; elongate, with rostrum only slightly tapered anteriorly, very slightly deflected, and somewhat inflated dorsolaterally; nasals extending well forward above premaxillae; maxillae dorsally in wide contact with frontals; laterally with infraorbital foramen simple, above posterior of P^3 in adult specimens, positioned well in advance of jugal; infraorbital canal elongate but variable, being 26·5–45·0 (n = 8); inferior process of anterior zygoma root moderately strong, extending ventrally almost to level of occlusion of cheek teeth. Lacrymal expanded onto facial surface, with superior and inferior lacrymal foramina on facial side of orbital rim; superior lacrymal tuberosity wide, bulbous, with inferior lacrymal tuberosity smaller, but prominent. Premaxillae with anterior narial floor declining posteriorly, wide; anterior premaxillary narial spines moderately strong. Labial foramen prominent, variably positioned, occasionally on ridge at edge of palate opposite posterior end of palatine foramen, but usually slightly mesiad to ridge, at premaxilla–maxilla suture. Palate entire, penetrated posteriorly by anterior palatine foramen and posterior lateral foramen; palatines moderately large, extending anteriorly to about level of M^3 in adult specimens. Jugal laterally excavated for superficial layer of masseter, with zygomatic arches converging somewhat anteriorly, with zygomatic crest posteriorly curving backwards and ventrally. Roof of braincase arched, with sagittal crest strongly defined in adult specimens owing to confluence of ridges passing posteriorly from above orbits. Subsquamosal foramen well defined, in strong squamosal sulcus separated below by continuation of zygomatic crest; squamosal widely separated from frontal, contributing with jugal, to glenoid fossa. Postzygomatic foramen prominent, at base of supratympanic sulcus in supratympanic fossa, immediately above external auditory meatus, separated from this by mastoid–squamosal crest. Mastoid foramen well defined towards upper limit of narrowly exposed mastoid. Post-glenoid process moderately strong, rather ovate posteriorly; post-glenoid foramen situated mesiad to process and at anterior limit of tympanic. External auditory meatus not well preserved, but moderately high; anteriorly bulla moderately crenulate;

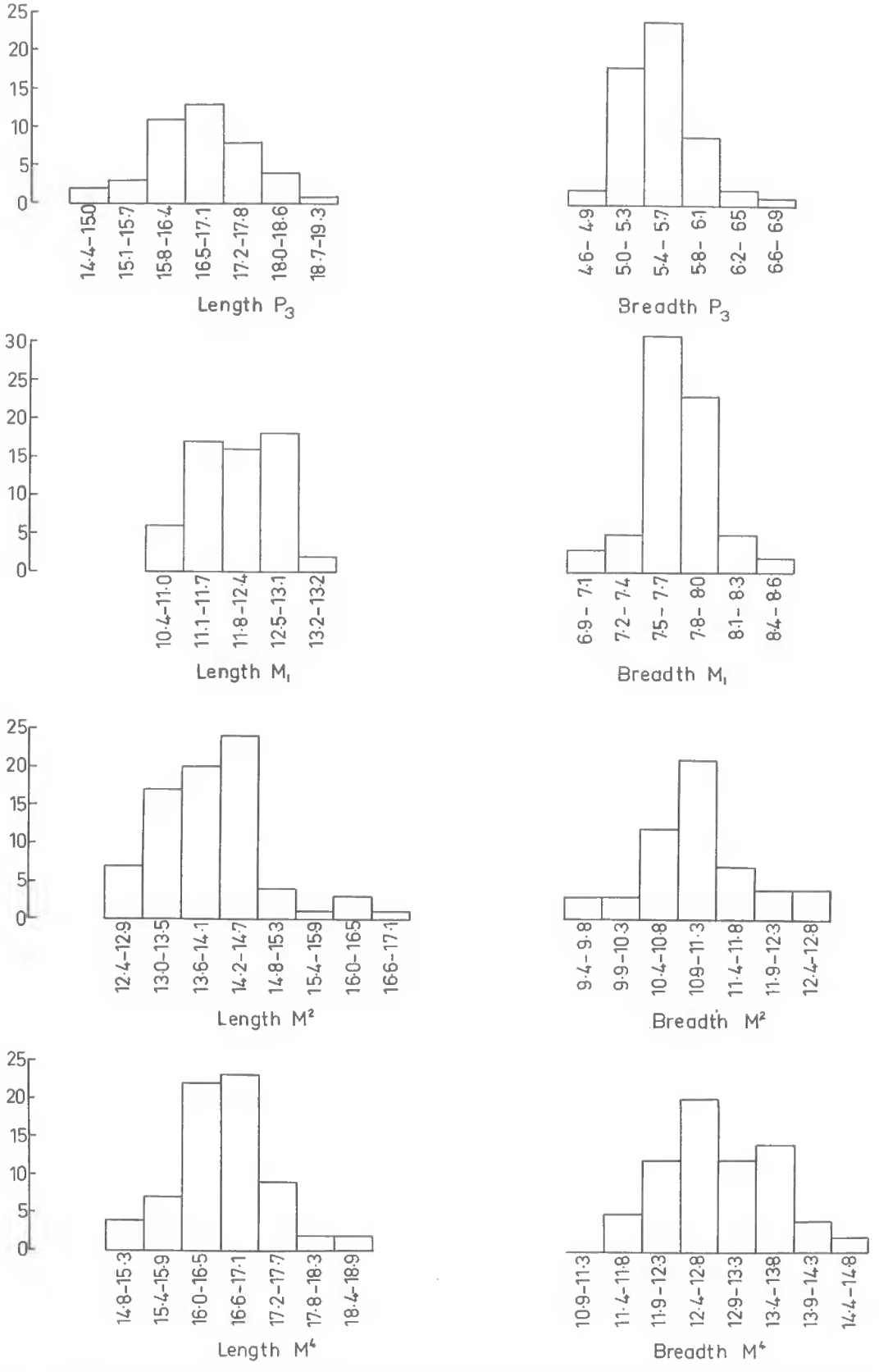

FIG. 5: Representative histograms for cheek teeth parameters in the *Protemnodon anak* Owen sample from the Pleistocene fluviatile deposits of the eastern Darling Downs.

alisphenoid bulla slightly inflated. Tympanic extending only slightly down paraoccipital process; processes broken in all specimens, but strong. Well defined ovale crest developed anteriorly from mesial wall of foramen ovale, bordering pterygoid cavity; crest continues laterally around foramen ovale to alisphenoid bulla; pterygoid cavity with several small fenestrations. Basisphenoid broadly grooved posteriorly at mid-line, this extending on to anterior of basioccipital; entocarotid canal posterior to basisphenoid–basioccipital suture; pterygoids partially overlap basisphenoid, being in sutural contact. Petrosal with exposed surface mesiad to eustachian canal gently concave posteriorly, sharply rounded anteriorly. Ridge extends mesially from paraoccipital process anterior to posterior lacerate foramen. Supraoccipital relatively low, wide, with lambdoidal crest extending posteriorly to marked extent with well defined supraoccipital depressions separated by moderate, rounded, median nuchal crest; inferior supraoccipital depressions absent. Condyloid foramen prominent.

TABLE 1

MANDIBULAR MEASUREMENTS FOR *Protemnodon anak* OWEN

Specimen	P_3	M_1	M_2	M_3	M_4
F3398*	16·2 × 6·0	— × 7·5	13·4 × 9·2	16·0 × —	16·6 × —
F3396**	16·8 × 5·4	10·5 × 7·5	13·5 × 9·4	16·3 × 10·5	17·8 × —

* Cast of holotype *P. anak*; ** Cast of holotype *P. og*.

Upper incisors broadly U-shaped in occlusal outline. I^1 large, with enamel surface from base to tip, longer than I^2 or I^3, axially curved; directed anteroventrally and somewhat mesially with tips approximated; labial surface curved, with slight vertical groove present near anterior extremity of tip, and stronger groove present about one-third distance along occlusal surface from posterior limit; anteromesial surface moderately curved distally, becoming more broadly curved towards crown base; mesial surface unenamelled, broadly curved, while posterior surface gently concave. I^2 slightly more elongate along occlusal surface in unworn teeth than I^1; labial surface at tip marked by broad groove, about one-third distance along crown from posterior limit; this occasionally offset from sharper groove towards base of crown, near mid-line of labial surface; occlusal surface not known in unworn condition, but with well defined groove extending posteriorly and ascending posterolabial crown surface for short distance; posterolabial portion of crown flared slightly. I^3 crown elongate distally, restricted basally, with broad, rounded, longitudinal groove towards base on labial surface and prominent diagonal groove across distal, posterolabial surface; this groove continues anteriorly along occlusal surface to terminate behind anterior surface; internally surface gently convex labially, but externally crown above occlusal groove flares posterolaterally.

TABLE 2

SUMMARY OF MEASUREMENTS FOR *Protemnodon anak* OWEN

Character	Maxillae					Mandibles				
	n	O.R.	$\overline{X}$	s	V	n	O.R.	$\overline{X}$	s	V
I_1 Depth						21	12·8–16·3	14·8	0·8715	5·89
P_2^2 length	3	11·6–13·5	12·5	—	—	20	10·2–11·8	11·0	0·4622	4·20
Maximum breadth	3	6·3– 7·5	7·1	—	—	23	4·6– 5·7	5·3	0·2557	4·82
DP_3^3 length	7	10·7–11·8	11·0	0·3719	3·38	32	9·0–11·8	10·6	0·5591	5·27
Breadth protoloph (-id)	6	8·0– 8·8	8·4	0·3193	3·80	25	5·3– 6·6	5·8	0·3187	5·49
P_3^3 length	32	16·5–18·9	17·7	0·6674	3·77	42	14·7–18·8	16·7	0·9059	5·42
Maximum breadth	36	7·4–10·1	8·4	0·7258	8·64	55	4·7– 6·6	5·4	0·3874	7·17
M_1^1 length	34	10·7–13·3	11·9	0·6896	5·79	59	10·4–13·5	12·0	0·7484	6·24
Breadth protoloph (-id)	36	9·1–11·2	10·0	0·4690	4·69	68	6·9– 8·6	7·7	0·3111	4·04
Height *	5	8·5–11·8	10·5	—	—	—	—	—	—	—
M_2^2 length	54	12·9–15·3	14·1	0·6073	4·31	85	12·3–15·3	13·9	0·7469	5·37
Breadth protoloph (-id)	46	10·3–12·8	11·5	0·5262	4·58	79	8·1–10·1	9·3	0·3948	4·25
Height *	9	8·9–12·6	10·9	1·4217	13·04	31	7·0– 9·0	7·9	0·5313	6·73
M_3^3 length	63	14·0–16·6	15·5	0·6257	4·04	98	13·8–16·8	15·5	0·6963	4·49
Breadth protoloph (-id)	51	11·0–13·7	12·3	0·6543	5·32	91	9·3–11·2	10·4	0·3911	3·76
Height *	16	7·7–12·4	10·9	1·1532	10·58	51	7·2– 9·1	8·3	0·5567	6·71
M_4^4 length	35	14·4–17·5	16·0	0·1833	5·08	75	15·0–18·0	16·5	0·6987	4·23
Breadth protoloph (-id)	34	11·3–13·7	12·4	0·6555	5·29	73	9·7–11·9	10·8	0·4691	4·34
Height *	12	7·8–11·8	9·5	1·2232	12·88	47	6·2– 8·7	7·6	0·5316	6·99

*Enamel height measured at hypocone and entoconid in unworn teeth.

C^1 rarely present, extremely small, vestigeal, laterally compressed.

P^2 relatively elongate, subovate to subtriangular in basal outline, being slightly to considerably broader posteriorly than anteriorly; longitudinal crest secant, moderately high, slightly concave labially or nearly straight; apex of paracone about one-quarter distance along crown from anterior point; crest transected by two sets of vertical labial and lingual ridges with production of cuspules at crest. Hypocone moderately high, being about one-half as high as metacone, united to metacone by strong, high labial ridge; posterior ridge from hypocone curves labially above base of crown to above metacone; shallow posterior fossette developed between this and ridge connecting posterior cusps. Anterior ridge from hypocone ascends sharply to form low lingual cingulum, converging anteriorly to above paracone, connected to it by slight ridge. Lingual cingulum gently convex lingually, occasionally sinuous, slightly tumid in lingual view; lingual basin shallow, subtriangular in shape, traversed by continuations of lingual ridges from cuspules at longitudinal crest. Slight anterolingual fossette formed in lingual basin. Weak ridge occasionally present at anterolingual base of crown.

DP^3 molariform, subrectangular in basal outline, slightly constricted across median valley; lophs moderately high, slightly bowed anteriorly; metaloph broader than protoloph. Anterior cingulum low, relatively narrow and short, with slight suggestion of forelink above axis of crown, at base of descending protoloph; accessory ridges occasionally present across cingulum; cingulum somewhat tumescent lingually. Strong, high ridge ascends anterolingually from paracone to labial limit of anterior cingulum, this being most anterior point of crown. Midlink moderately strong and high, curving posterolabially from protocone to unite with short ridge from near mid-point of metaloph, above median valley; uniting with slight ridge from anterior surface of metaloph, partially closing off labial moiety of valley, about half-way between midlink and labial margin. Median valley sharply V-shaped labially and lingually. Strong ridge curves posterolabially from hypocone to base of crown above metacone, while weaker ridge curves posterolingually from metacone towards crown base, terminating labiad to axis; ridge from hypocone somewhat posteriorly flared, with slight posterior fossette formed at axis of crown.

P^3 elongate, being longer than any molar, usually somewhat broader posteriorly than anteriorly; crown in occlusal view frequently markedly concave labially, but generally straight or slightly convex lingually; longitudinal crest secant, moderately high, markedly to slightly concave labially; apex of paracone about one-fifth distance along crown from anterior point; crest transected by three (51 %, n = 37), four (46 %, n = 37), or occasionally two (3 %, n = 37) sets of vertical labial and lingual ridges, with production of cuspules at crest. Hypocone moderately high, being about three-quarters as high as metacone, united to metacone by strong, high, labial ridge; posterior ridge from metacone ascends towards crown base; posterior ridge from hypocone curves labially to above metacone; well defined posterior fossette developed between this and ridge connecting posterior cusps. Anterior ridge from hypocone usually ascends sharply to form low, lingual cingulum, generally converging anteriorly to above paracone, connected to it by slight vertical ridge. Lingual ridge from first cuspule along crest from paracone generally prominent, separating anterior one-third of cingulum and lingual basin as slight anterolingual

pocket; occasionally other pockets developed posterior to this; in lingual aspect, cingulum markedly tuberculate, at points of origin of lingual ridges to crest cuspules. Lingual basin relatively shallow, separated by extensions of lingual ridges from crest. Base of crown somewhat tumid, particularly anteriorly.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, unconstricted or slightly constricted across median valley; lophs moderately high, slightly bowed anteriorly; metaloph slightly broader than protoloph in M^1, approximately equal or slightly narrower in M^2 and occasionally M^3, and markedly narrower in remaining M^3 and M^4. Anterior cingulum low, relatively narrow and short, sometimes broader, descending labially; generally no trace of forelink present; cingulum frequently somewhat tumescent lingually. Strong, high ridge ascends anteriorly from paracone to labial limit of anterior cingulum, with anterior margin of cingulum broadly rounded between labial and lingual limits; slight fossette usually present in anterolingual portion. Midlink moderately strong and high, curving posterolabially from protocone to unite with short ridge from near mid-point of metaloph, above median valley; strong ridge curves posterolingually from paracone usually on to labial surface of midlink, occasionally uniting with slight, variable ridge ascending anterolingually from metacone. Median valley narrowly U-shaped in labial moiety, more broadly U-shaped lingually; base of valley not markedly ascending labially or lingually from midlink. Strong, slightly flared ridge curves posterolabially from hypocone to base of crown slightly mesiad to posterolabial limit, uniting with weaker ridge ascending slightly posterolingually from metacone. Slight posterior fossette formed slightly labiad to axis.

TABLE 3

MEASUREMENTS FOR UPPER INCISORS IN *Protemnodon anak* OWEN

Specimen	F2540	F5176	F651	F2103	F5028	F3672 rt.	F3672 lt.
Length I^1	—	9·1	10·0	9·6	9·5	9·0	9·3
Length I^3	13·4	14·1	11·5	14·3	12·3	14·5	14·5

DISCUSSION: Owen (1859) introduced the name *Macropus anak* as a *nomen nudum* and later (Owen, 1873) used the combination *Protemnodon anak* in abstract in like fashion. The name *Protemnodon anak* was validated by Owen (1874) and dates from that time. Knowledge of the species is currently restricted to cranial remains.

In describing *P. anak*, Owen (1874) emphasized the comparatively broader trigonid basin (prebasal ridge) in M_4 in the holotype specimen and in the specimen figured (Owen, 1874, pl. 25, fig. 3). This feature is found to be somewhat variable where sufficient material is available to more fully assess the range in morphological variation present. As indicated by Owen (1874) the presence of a posterior cingulum (postbasal ridge) is variable, but it does prove to be present in most instances. Where absent in one molar, it is usually present in others of the same series.

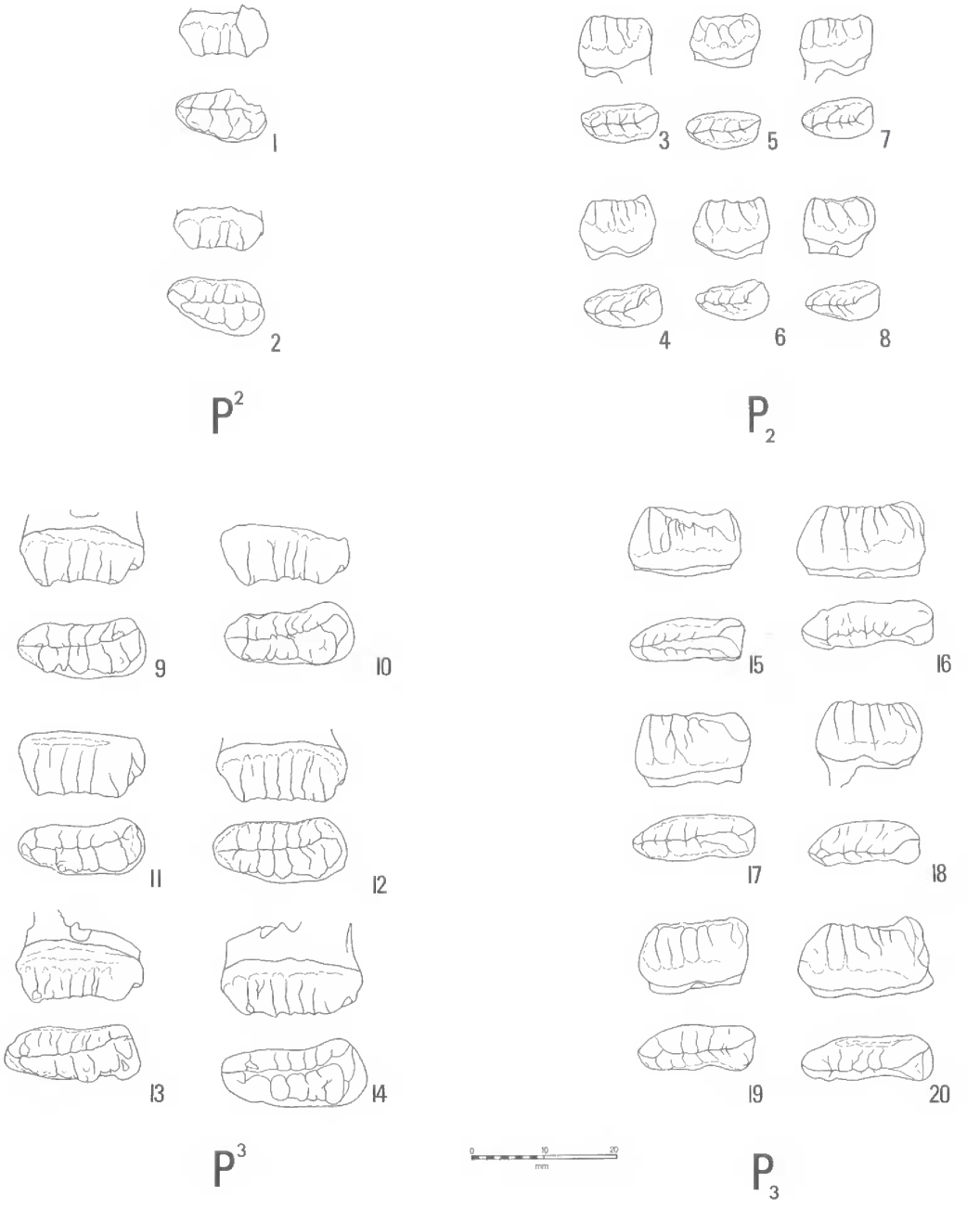

FIG. 6: Morphological variation in the premolar teeth in *Protemnodon anak* Owen. Lateral view above, occlusal view below. 1, right P^2 reversed, F5060; 2, left P^2, F3677; 3, left P_2, F4844; 4, left P_2, F3046; 5, right P_2 reversed, F4818; 6, left P_2, F3644; 7, left P_2, F4832; 8, left P_2, F4817; 9, right P^3 reversed, F5200; 10. left P^3, F4977; 11, right P^3 reversed, F3667; 12, left P^3, F5197; 13, left P^3, F5045; 14, right P^3 reversed, F5178; 15, right P_3 reversed, F3003; 16, left P_3, F2998; 17, right P_3 reversed, F3017; 18, left P_3, F3006; 19, right P_3 reversed, F4900; 20, left P_3, F4871.

Owen (1874) utilized several features to justify the separation of *P. og* Owen from *P. anak* here considered synonymous. These included the strength of the molar links and the inclination of the diastemal crest anterior to P_3. Complete intergradation exists where the sample examined is sufficiently large. *P. og* was further distinguished from *P. anak* by its larger size. As indicated in the accompanying representative histograms, illustrated in Figure 5, no major size distinctions are present in the material. Measurements for the holotype specimens of *P. anak* and *P. og* are presented in Table 1. Table 2 presents the summaries of measurements for mandibular and maxillary specimens of *P. anak* and indicates only slight to moderate variation as expressed by the Coefficient of Variation (V) for all measurements except the height of enamel at the hypocone in unworn upper molar teeth. Generally, the values for V are consistent with those determined for the living Grey Kangaroo, *Macropus giganteus* Shaw and the Sandy Wallaby, *M. agilis* (Gould), by Bartholomai (1971) and for other fossil kangaroos from the Darling Downs area (Bartholomai, 1967, 1970). Slight age differences may be present between localities from which the sample was drawn but no control to evaluate the possible effect of this is possible at this time because of a lack of statistically significant samples from different sites.

The abnormal values for V in the heights of upper molar teeth are not mirrored in those for the corresponding lower teeth and the disparity appears to result not from an actual difference in height of crown, but from differences in the level of enamelization of the crown in the upper molars. Moderately high values for the Coefficient of Variation for the breadths of P_3 and P^3 reflect true variation in these characters in *P. anak*, also shown to be present in the living macropodids considered by Bartholomai (1971). This is true regardless of the fact that the permanent premolars in *P. anak* are large, functional teeth which have not been found excluded from the tooth row by progression. A foreward movement of the tooth row is present, but it is not as marked as in the larger species of the genus *Macropus*. Morphological variation for the premolars in *P. anak* is illustrated in Figure 6.

Of interest is the fact that an upper canine is preserved in F3672, the only specimen in the Queensland Museum collections to present this tooth. It is small and vestigial, but morphologically it is similar to the C^1 developed in other macropodids. Its presence has not previously been recorded in *Protemnodon*.

The upper incisors, although not preserved in statistically useful numbers, present features which suggest their use in the separation of at least some of the species of *Protemnodon*, particularly in the separation of *P. anak* from specimens here referred to *P. roechus* Owen. Stirton (1963) indicates the marked discrepancy which occurs in *Protemnodon* in the lengths of the occlusal surfaces in I^1 when compared with the lengths in I^3, but suggests that there appears to be intergradation between the extremes. While variation certainly exists, the present sample of *P. anak*, measurements for which are tabulated in Table 3, shows no overlap of values with those for *P. roechus* (Table 11). It is unfortunate, however, that upper incisors are at present unknown in the Queensland Museum collections in the medium to large sized species *P. brehus*, derived from the same sediments as *P. anak* and *P. roechus*.

A similar difference exists in the depth of the lower incisors, although the comparisons are valid only in relatively unworn specimens because of the extreme wear facets developed in these teeth. A summary of measurements for the depth of I_1 in *P. anak* is presented in Table 2. This shows marked differences from that for the corresponding tooth in *P. roechus,* results for which are presented in Table 10. However, some variation is evident within samples in these species and, in the absence of lower incisors in *P. brehus* the taxonomic value of these teeth is difficult to assess.

The crania of *P. anak* represented in the present sample agree well with the description provided in Stirton (1963). From his illustrations, it appears certain that the subject of his figure 2, AM F2221 is of *P. anak*. It has been shown above, however, that AM F16490, illustrated by Stirton (1963, fig. 3) is clearly not referable to this species. A reconstruction of the skull of *P. anak,* based on the present sample, is here presented in Figure 2.

Owen (1876, 1877) has described several fourth metatarsals and referred these to *P. anak* with no apparent justification. These are totally dissimilar in proportions to the metatarsals of *P. otibandus* Plane, illustrated by Stirton (1963), from the Pliocene Otibanda Formation in New Guinea. Proportionately similar metatarsals to those found in *P. otibandus* are present in the Pleistocene fluviatile deposits of the eastern Darling Downs but no attempt has been made at this time to sort these. It is certain, however, that the metatarsals in *P. anak* are represented in this disassociated material and that the specimens referred by Owen (1876, 1877) have been incorrectly assigned.

P. anak is the best represented species of *Protemnodon* in the Queensland Museum collections and has been recorded from numerous localities in the Pleistocene fluviatile deposits of the eastern Darling Downs. It is, as yet, unknown from other Queensland localities, although a mandibular specimen, F2496, from Chinchilla, appears to be referable to the species. Preservation of this specimen is unlike that normally associated with material derived from the Chinchilla Sand (Woods, 1956), and it is probable that it was collected from Pleistocene terrace deposits in the area.

Tedford (1967) indicates the presence of a species of *Protemnodon* smaller than *P. brehus* Owen from the Scotchtown Cave assemblage in northwestern Tasmania (Gill and Banks, 1956), but as no illustration or description has yet been presented for this material its specific identity must remain in doubt. A mandibular ramus from King Island, in Bass Strait, morphologically similar to the Scotchtown Cave material (Tedford, 1967), has been referred to *Macropus anak* by Scott and Lord (1924), who state that it is closely comparable with the specimen figured by Owen (1874, pl. 25, figs. 7–10) as *P. anak*. As such, it is very likely that it is referable to this species. However, the ramus was not figured and again the specific determination cannot be resolved at this time.

It is apparent from the material figured and described by Stirton (1963) that *P. anak* is present in the Wellington Caves fauna and several specimens of this species were located in the small sample of *Protemnodon* currently available in the Australian Museum collections and which unquestionably came from that deposit. *P. anak* is widespread in New South Wales and is present from Weetalabah Creek, near Coolah; Breeza; Copes Creek; Huntsgrave, Keepit, in a deposit thirty feet below the surface; in a well at Parsens

Hill Plain, Warrah; Abercrombie Caves; and from nine miles west of Attunga. Morphological variation exhibited within this material is similar to that seen in the Queensland sample, but too few specimens are available to allow statistical comparison of samples to be undertaken.

In Western Australia, *Macropus anak* is recorded by Glauert (1912) from the Mammoth Caves in the southwest, but he does not illustrate either of the two mandibular fragments mentioned. From his discussion, it appears that the material may not be of *P. anak* and that it may be comparable with *P. brehus*. The specimens later recorded by Glauert (1921) as *Macropus anak*, from Quambun Station, Fitzroy River Crossing in northwestern Western Australia, are also doubtfully referable to the species until checked.

Stirton *et al.* (1961) recorded the presence of a small species of *Protemnodon*, comparable with *P. og*, from the Pleistocene Malkuni Fauna of the Katipiri Formation from the Tirari Desert, in northeastern South Australia, but suggested the material from the older Kanunka Fauna from that Formation may be distinct.

It is thus apparent that although the species may be widely represented throughout Australia, the distribution is largely obscured by uncertainty in identification of referred specimens.

Protemnodon brehus (Owen, 1874)

(Plates 13–15)

Sthenurus brehus Owen, 1873, p. 128 (*nomen nudum*).
Protemnodon mimas Owen, 1873, p. 128 (*nomen nudum*).
Sthenurus brehus Owen, 1874, pp. 272-4, pl. 27, figs. 5–9; 1876 (*partim*), pp. 212–8, pl. 28, figs. 1–3; 1877, pp. 424–6, 442, 444, pl. 87, figs. 5–9; Etheridge Jnr., 1892, p. 678; Simpson, 1930, p. 77.
Protemnodon mimas Owen, 1874, pp. 278–80, pl. 26, figs. 1–3; 1877, pp. 431–3, 447–9, pl. 86, figs. 1–3; Etheridge Jnr., 1892, p. 677; Palmer, 1904, p. 883; Simpson, 1930, p. 76; Stirton, 1963, p. 139, fig. 14a.
Macropus brehus (Owen): Lydekker, 1887, pp. 207, 309, 311; Lydekker, 1894, pp. 256–7; Lydekker, 1896, p. 256.
Halmaturus anak (Owen): De Vis, 1895 (*partim*), pp. 104–9.
Protemnodon brehus (Owen): Stirton, 1963, p. 141, fig. 15b; Tedford, 1967, pp. 97–109, figs. 25–6.

MATERIAL: F3400, cast of holotype of *P. brehus* (Owen), British Museum (Natural History) No. 43303a, partial palate with left M^1–M^4, right M^3–M^4, adult, Wellington Valley, N.S.W., figd Owen (1874, pl. 27, figs. 5–6; 1877, pl. 87, figs. 5–6).

F3395, casts of holotype of *P. mimas* Owen, British Museum (Natural History) No. 43351, partial left mandibular ramus, with P_3–M_4, adult, Gowrie Creek, SE. Q., figd Owen (1874, pl. 26, figs. 1–3; 1877, pl. 86, figs. 1–3).

Five juvenile mandibular rami, 19 adult mandibular rami, 2 isolated lower teeth, 2 juvenile maxillae, 13 adult maxillae, and 4 isolated upper teeth from the following localities in the eastern Darling Downs: King Creek; King Creek, at M.R. 873335 Clifton 1 mile map; King Creek, at M.R. 055459 Clifton 1 mile map; Ravensthorpe, Pilton; 'Sharrow' (Harrow, Cambooya); Gowrie; Jimbour Creek, near Dalby; Kaimkillenbun, near Dalby, 54 feet below surface; and from the eastern Darling Downs (particular localities unspecified).

Other Queensland localities represented include 'Coreena', between Barcaldine and Aramac, C.Q.; and 'Planet Downs', near Gregory Downs, NE. of Camooweal, N.W.Q., 17 feet below surface.

SPECIFIC DIAGNOSIS: Large species, generally larger than *P. anak*.

Mandible relatively deep, with symphysis elongate; symphysis elevated to approximately 20° to base of mandible; lateral groove extends posteriorly to below M_2–M_3, moderately close to alveolar margin.

P_2 relatively elongate, with longitudinal crest high, nearly straight except in posterior one-quarter where crest markedly flexed lingually; crest transected by one set of near vertical labial and lingual ridges. DP_3 unconstricted across talonid basin; trigonid basin very broad; posterior cingulum strongly developed, broad. P_3 relatively elongate, broader posteriorly, with longitudinal crest high; crown usually strongly constricted lingually at posterior one-third; crest straight but rapidly curving lingually in posterior extension, transected by three to four sets of vertical labial and lingual ridges; cuspules present. Lower molars slightly constricted across talonid basin, with lophids high; trigonid basin and anterior cingulum broad; anterolabial fossette present; posterior ridge from metaconid not developed; slight ridge occasionally present from entoconid; posterior cingulum well defined, broad.

P^3 relatively elongate, being generally shorter than length of M^4; crown slightly concave labially in occlusal view; longitudinal crest high, slightly concave labially; crest transected by three or four sets of vertical labial and lingual ridges; cuspules present; lingual cingulum occasionally continues anteriorly from above paracone to near anterior of crown; cingulum markedly sinuous in lingual view. Upper molars slightly constricted across median valley, with high lophs; anterior cingulum broad, anteriorly broadly curved; forelink generally absent; anterior ridge from paracone strong, usually passing to limit of cingulum; relatively strong ridge curves posteriorly from paracone, often continuous across valley with lesser ridge from metacone; base of median valley near planar transversely; lingual limit of valley usually not tuberculate.

DESCRIPTION: Mandible relatively deep and thick; base of symphysis elevated at approximately 20° to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit relatively deep, near posterior symphysial limit; diastema relatively elongate with crest acute, becoming slightly less so anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen relatively large, ovate, close to diastemal crest. Ramus with well defined, shallow, lateral groove extending posteriorly to below M_2–M_3, often disrupted by roots of P_3; groove positioned about one-quarter distance from alveolar margin to base of ramus. Diagastric process bounded above by shallow diagastric fossa; this fossa separated above from shallow depression opening posteriorly into large pterygoid fossa. Post-alveolar shelf short, with shelf angle usually not well developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above mandibular foramen. Masseteric crest raised to about level of alveolar margin; masseteric foramen moderately large, with masseteric fossa relatively deep. Coronoid process, condyle and angle of mandible not preserved in any specimen.

I_1 not preserved.

P_2 relatively elongate, slightly broader posteriorly than anteriorly. Longitudinal crest secant, nearly straight, except in posterior one-quarter, where crest is markedly

flexed lingually; crest transected by one major set of near-vertical labial and lingual ridges; anterior cuspid of crest well defined. Base of crown slightly tumid, especially lingually.

DP_3 molariform, subrectangular in occlusal view, unconstricted across talonid basin, with protolophid narrower than hypolophid. Trigonid basin very broad, elongate. Forelink well defined, extending anteriorly to near midpoint of relatively low anterior cingulum; slight fossette present at margin of labial moiety of trigonid basin. Midlink moderately strong, extending anteriorly from hypolophid to near midpoint of protolophid, across talonid basin; basin shallowly U-shaped both labially and lingually. Moderate ridge descends posteriorly from entoconid to lingual margin of strong posterior cingulum; posterior cingulum broad, extending and descending slightly from posterolingual crown margin to posterolabial margin.

P_3 relatively elongate, high, robust, deeply rooted; crown suboval to subtriangular in occlusal view, usually broader posteriorly than anteriorly and tapering anteriorly, but with slight to marked lingual constriction at about posterior one-third. Crest secant, nearly straight or slightly sinuous, markedly curving lingually in its posterior extension; crest transected by three or occasionally four sets of vertical labial and lingual ridges with production of cuspules at crest; strength of ridges and cuspules decreases posteriorly. Anterior ridge from anterior cuspid of crest descends at moderately high angle to crown base. Base of crown slightly tumid. Height of enamel usually similar anteriorly and posteriorly.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, usually slightly constricted across talonid basin; lophids high, slightly convex posteriorly, with hypolophid broader than protolophid in M_1 and M_2, approximately equal in M_3 and narrower in M_4. Trigonid basin broad, elongate, its length approximating distance between lophids. Forelink relatively high, moderately strong, curving anterolingually from protoconid to near midpoint of low, broad, anterior cingulum; cingulum gently curved to below protoconid, but more abruptly curved lingually; trigonid basin normally descends at about same angle labially and lingually from forelink, with slight anterolabial fossette formed at margin of labial moiety; very slight ridge descends anteriorly from metaconid but posterior ridge is not developed; this is sometimes accompanied by a posterolabial groove; midlink moderately high and strong, curving anterolingually from hypoconid to unite with short ridge from near midpoint or slightly labiad to axis of protolophid, above talonid basin; slight ridge occasionally present but sometimes quite strongly developed, descending anterolabially from entoconid, into talonid close to midlink; talonid basin sharply U-shaped, occasionally becoming more angular, descending at moderate angle labially and lingually from midlink. Slight posterior ridge from entoconid usually

TABLE 4

MANDIBULAR MEASUREMENTS FOR *Protemnodon brehus* (OWEN)

Specimen	P_3	M_1	M_2	M_3	M_4
F3395*	16·5 × 6·4	13·4 × —	15·3 × 10·6	17·9 × 12·1	19·7 × 12·3

* Cast of Holotype *P. mimas*.

present descending to unite with lingual limit of posterior cingulum, frequently mirrored by similar ridge from hypoconid; posterior cingulum well developed, nearly horizontal, broad, extending over most of posterior of base of hypolophid. Base of crown rarely tumid.

Cranium known only from maxillary fragments. Inferior process of anterior zygoma root moderately strong, extending to about level of occlusion of cheek teeth; infraorbital canal moderately elongate; palate entire, perforated by anterior palatine foramen and posterior lateral foramen.

DP^3 imperfectly preserved. Only upper permanent cheek teeth sufficiently well known to be described.

P^3 elongate, being generally slightly shorter than length of longest molar, slightly to moderately broader posteriorly than anteriorly; crown in occlusal view, slightly concave labially, slightly convex to nearly straight or even concave lingually; longitudinal crest secant, slightly concave labially, moderately high. Apex of paracone about one-fifth distance along crown from anterior point; crest transected by three or occasionally four sets of vertical labial and lingual ridges, with production of cuspules at crest; cuspules decrease in strength posteriorly, as do transecting ridges. Hypocone moderately strong, united to above metacone by strong, high, labial ridge; posterior ridge from metacone ascends towards crown base; posterior ridge from hypocone curves labially to above metacone; well defined posterior fossette developed between this and ridge connecting posterior cusps; anterior ridge from hypocone curves lingually and ascends sharply to form low lingual cingulum, generally only slightly converging anteriorly to above paracone, but occasionally further extending anterior to this point to unite with marked anterolingual ridge descending from anterior ridge from paracone; cingulum occasionally disrupted anteriorly; paracone connected to cingulum by moderately strong lingual ridge; in lingual view, cingulum markedly sinuous in outline. Ridges from cuspules along crest usually cross relatively shallow lingual basin, to cingulum; anterolingual fossette, posterior to ridge from paracone to cingulum, frequently well developed. Base of crown slightly tumid; enamel height usually slightly greater anteriorly than posteriorly.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley; lophs moderately high, slightly bowed anteriorly; metaloph broader than protoloph in M^1, approximately equal in M^2 and M^3, and narrower in M^4. Anterior cingulum low, broad, short, near planar transversely; generally no trace of distinct forelink present, but ridgelets frequently pass from base of protoloph onto cingulum; anteriorly, cingulum flattened or very broadly curved; relatively strong ridge ascends from paracone, usually uniting with labial limit of cingulum, delimiting extent of cingular shelf; anterolingual fossette generally present at lingual limit of cingular shelf. Midlink moderately strong, relatively high, curving posterolabially from protocone to unite with short ridge from near mid–point of metaloph, above median valley; relatively strong ridge curves posterolingually from paracone to near midlink, often continuous across median valley with slight anterolingual ridge from metacone; labial moiety of median valley narrowly U-shaped, lingual moiety broadly U-shaped; base of valley near planar transversely; lingual limit of valley generally smooth, but very occasionally tuberculate. Strong, slightly flared ridge curves posterolabially from hypocone to base of crown slightly

mesiad to posterolabial limit, uniting with weaker ridge ascending slightly posterolingually from metacone. Slight posterior fossette formed between ridges and base of metaloph, labiad to crown axis.

TABLE 5
MAXILLARY MEASUREMENTS FOR *Protemnodon brehus* (OWEN)

Specimen	M^2	M^3	M^4
F3400 lt.*	15·6 × 14·6	19·1 × —	17·6 × 14·1
rt.*	—	— × 14·2	17·4 × 13·9

* Cast of Holotype *P. brehus*.

DISCUSSION: *Sthenurus brehus*, described by Owen (1874), is the only species now referable to the genus *Protemnodon* based on maxillary remains, and represents the only Pleistocene species based on material collected from an area outside the Pleistocene fluviatile deposits of the eastern Darling Downs. Because of problems of association of maxillary and mandibular specimens of the genera *Sthenurus* and *Protemnodon*, the description of *S. brehus* contributed to the early confusion detailed by Stirton (1963). Both Lydekker (1887) and De Vis (1895) recognized the correct relationships of the species but referred it to the genera *Macropus* and *Halmaturus*, respectively. The former generic concept is here considered too broad, while the latter is nomenclaturally unavailable, constituting as it does a junior secondary homonym of *Macropus*. No doubt exists regarding the relegation of the species to the genus *Protemnodon*. The limits placed on the species by Lydekker (1887) are considered correct, whereas those of De Vis (1895), who referred all the Queensland material to a single species, *Halmaturus anak*, are too wide.

Queensland Museum specimens collected from the Darling Downs deposits have been checked against topotypic specimens in the Australian Museum, Sydney, from the Wellington Caves area and against a cast of the holotype, British Museum (Natural History) No. 43303a, and have been found to be morphologically inseparable. Minor size differences, although not able to be assessed statistically, appear to be within the limits expected for a single species.

Owen's (1874) description of *P. brehus* was based on two specimens, the holotype and a paratype maxillary fragment from the Wellington Caves, now numbered British Museum (Natural History) No. 43653. Tedford (1967) provides a redescription of this latter specimen (figured Owen, 1874, pl. 27, figs. 7–9). This differs to some extent from the material here referred, particularly in the lack of well defined subdivision of the lingual basin by ridges between the base of the longitudinal crest and the lingual cingulum. This character proved variable in the sample considered by Tedford (1967) from Lake Menindee, New South Wales, and it is apparent that the same is true of the Queensland sample. It is more usual, however, for the basin to be subdivided.

Among material subsequently described and figured by Owen is a partial skull which provides additional information on the morphology of *P. brehus*. This specimen,

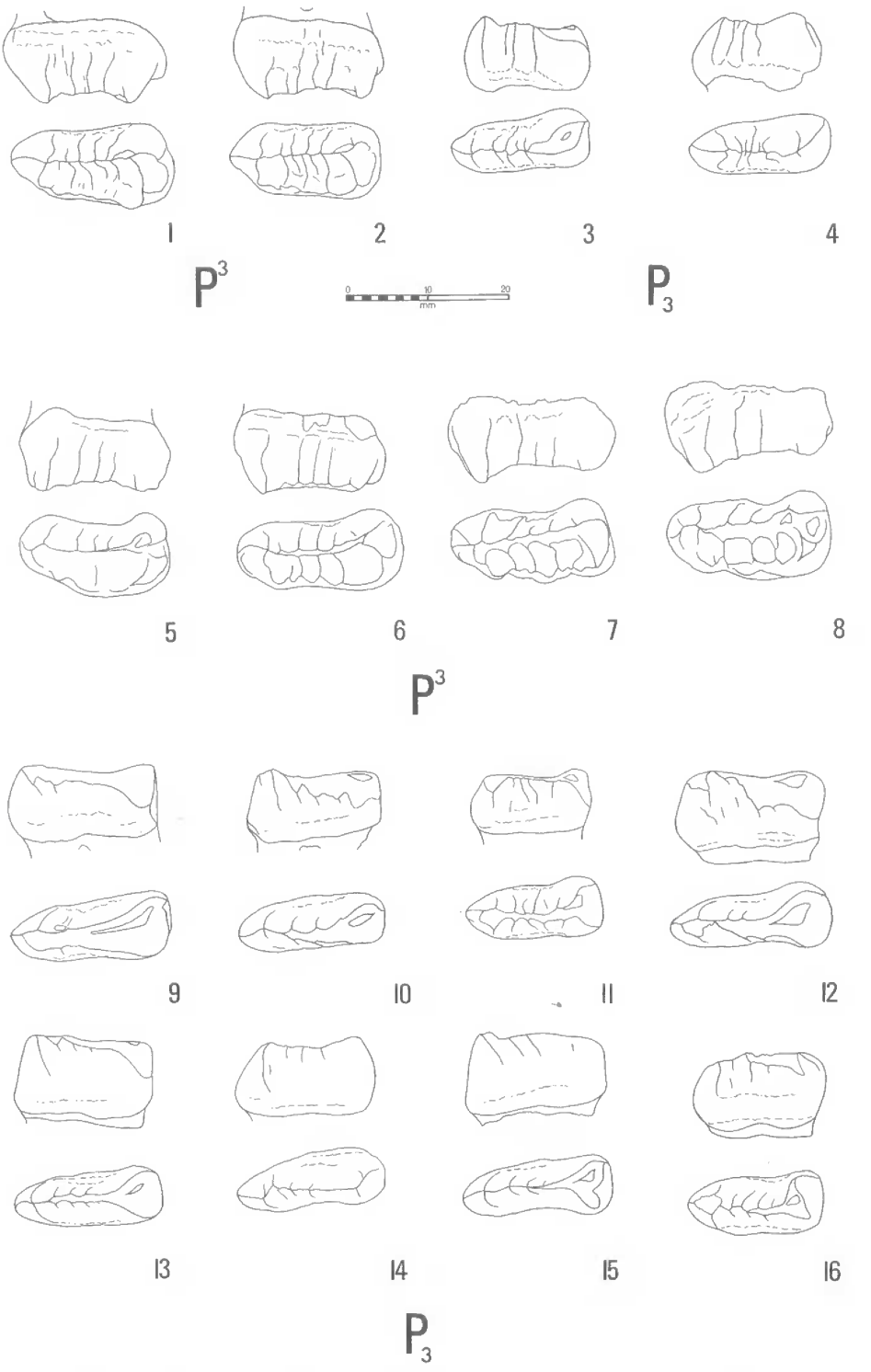

FIG. 7: Morphological variation in the permanent premolar teeth in *Protemnodon brehus* (Owen), (1–4) and *Protemnodon roechus* Owen (5–16). Lateral view above, occlusal view below. 1, left P^3, F4795; 2, left P^3, F4954. 3, left P_3, F4941; 4, right P_3 reversed, F3651; 5, right P^3 reversed, F1384; 6, left P^3, F1849; 7, left P^3, F4971; 8, right P^3 reversed, F4955; 9, right P_3 reversed, F5077; 10, left P_3, F5; 11, right P_3 reversed, F3009; 12, right P_3 reversed, F5078; 13, right P_3 reversed, F3033; 14, left P_3, F3007; 15, right P_3 reversed, F3019; 16, right P_3 reversed, F5087.

TABLE 6

SUMMARY OF MEASUREMENTS FOR *Protemnodon brehus* (OWEN)

Character	Maxillae					Mandibles				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
P_2 length	—	—	—	—	—	1	11·5	11·5	—	—
Maximum breadth	—	—	—	—	—	1	5·9	5·9	—	—
DP^3_3 length	1	12·3	12·3	—	—	1	11·6	11·6	—	—
Breadth protoloph (-id)	—	—	—	—	—	1	7·8	7·8	—	—
P^3_3 length	9	18·1–19·8	19·2	0·5339	2·78	10	16·4–18·7	17·7	0·8478	4·79
Maximum breadth	10	9·3–10·6	10·0	0·5011	5·01	9	6·5– 8·2	7·1	0·4847	6·83
M^1_1 length	6	12·7–14·6	13·6	0·6899	5·07	9	12·0–14·8	13·5	0·9151	6·78
Breadth protoloph (-id)	4	12·0–12·7	12·3	0·2943	2·39	6	9·3–10·6	9·9	0·5099	5·16
M^2_2 length	14	14·8–17·0	16·3	0·6251	3·83	14	14·9–18·0	16·3	0·9231	5·66
Breadth protoloph (-id)	11	13·4–14·6	14·0	0·3420	2·44	11	10·6–12·7	11·5	0·6299	5·48
Height *	4	10·6–13·9	12·2	1·3699	11.23	3	9·6– 9·9	—	—	—
M^3_3 length	18	16·2–18·1	17·5	0·5850	3·34	15	16·7–19·9	18·2	0·8311	4·57
Breadth protoloph (-id)	15	13·7–15·1	14·5	0·4017	2·77	13	11·9–13·2	12·6	0·4031	3·20
Height *	6	9·7–13·0	11·6	1·1849	10·21	6	8·2–10·6	9·7	0·8000	8·25
M^4_4 length	12	17·3–19·1	18·2	0·5885	3·23	11	18·1–20·6	19·2	0·8614	4·49
Breadth protoloph (-id)	11	13·7–15·0	14·3	0·4147	2·90	9	11·6–13·5	12·7	0·6041	4·76
Height *	4	9·8–12·2	11·1	1·1369	10·24	4	8·7–10·0	9·4	0·6055	6·44

* Enamel height measured at hypocone and entoconid in unworn teeth.

numbered 47833 in the British Museum (Natural History) collections possesses a full but worn compliment of upper incisors and a right P^3–M^1. Sufficient of the cheek teeth is preserved to indicate the correct reference of this specimen, collected from Clifton, Darling Downs, to *P. brehus*. The upper incisors appear to be somewhat intermediate in morphological detail between *P. anak* and *P. roechus* described below. I^1 is considerably larger than in *P. anak* compared with I^2 and I^3. In lateral view the occlusal surfaces are angled considerably from the horizontal, more so than in *P. roechus*, while the diastemal length is somewhat shorter than in that species. The nasals appear to have been considerably retracted, similar to the situation in *P. roechus* and this conclusion is supported by a cranial specimen of *P. brehus* from Lake Tandau in the Lower Darling region of New South Wales, housed in the collections of the Western Australian Museum.

Lydekker (1887) has indicated that the cranial specimen illustrated by Owen (1874, p. 27, figs. 1–4) as *P. mimas* is of *P. brehus* but the specimen is not sufficiently well illustrated to allow this conclusion to be supported confidently. It is doubtful whether the premaxillae figured by Owen (1876, pl. 28, figs. 1–3) as *P. brehus* relate to this species. Morphologically, these appear referable to *P. roechus*.

Association of mandibular remains with the referred maxillary specimens has been achieved largely through considerations of size as well as morphology. Mandibular rami in the Queensland Museum collections here referred to *P. brehus* are morphologically identical with the holotype of *P. mimas*, described by Owen (1874) from Gowrie Creek, Darling Downs and, as suggested by Lydekker (1887), this species is here regarded in synonymy with *P. brehus*. Measurements for holotype specimens of *P. brehus* and *P. mimas* are presented in Tables 4 and 5.

Summaries of measurements for the Queensland sample of *P. brehus*, presented in Table 6, generally indicate only slight to moderate variation as expressed by the Coefficient of Variation, and are largely consistent with the values for V present in other fossil macropodids from the area, and in the control samples of recent macropodids the results of which were published in Bartholomai (1971). As with other species of *Protemnodon* here considered, the breadth of P^3 is moderately variable, whereas the heights of enamel at the hypocone in unworn teeth often suggest a high degree of variation. As suggested previously, however, high values of V for enamel height are influenced not by actual crown heights but by wide flexibility in the level of enamelization of the crown. Measurements for lengths and breadths of teeth generally fall within the values for V indicated by Simpson *et al.* (1960), as consistent for a single fossil species from slightly differing statigraphic levels. Figure 7 illustrates some morphological variation present in permanent premolars.

Measurements for specimens referred to *P. brehus* by Tedford (1967) from Lake Menindee, often indicate sizes exceeding these for specimens in the Queensland sample. Because of the relatively small size of Tedford's (1967) samples, the statistical significance of these size differences cannot be evaluated. It is possible that there could be some representation in the Lake Menindee sample of the large species, *P. roechus*, considered below, and this could account for some of the larger values present in teeth dimensions.

Further morphological evidence more characteristic of *P. roechus*, particularly the tuberculation at the lingual extremity of the median valley in upper molars, is also apparently present to some extent in the sample.

Comparison of the Queensland material with a limited selection of specimens from the Bingara deposits, northern New South Wales, held in the collections of the Australian Museum, Sydney, indicates the presence of possible minor differences related to the breadth of anterior lower permanent cheek teeth. Morphologically, the Bingara and Darling Downs samples are identical and the size differences, relating as they do to a limited number of specimens in the available Bingara sample, are not considered sufficient to justify a suggestion of taxonomic distinction. Unfortunately, the maxillary sample available contains posterior cheek teeth only and the presence of minor size differences in the anterior cheek teeth cannot be confirmed in the upper dentition. Measurements for the Bingara material are included in Tables 7 and 8.

TABLE 7

MANDIBULAR MEASUREMENTS FOR *Protemnodon brehus* (OWEN)—BINGARA, N.S.W. SAMPLE

Specimen	P_3	M_1	M_2	M_3	M_4
AM MF1092	—	—	—	18·0 × 12·2	—
AM F55351	—	—	—	—	19·4 × 13·3
AM F55352	—	—	—	18·6 × 12·4	—
AM MF1094	—	—	16·3 × 10·9	—	—
AM F55353	17·7 × 7·1	13·4 × 9·8	—	—	—
AM F55354	—	—	16·8 × 11·4	—	—
AM F55355	16·8 × 6·2	13·7 × 9·2	—	—	—
AM MF1057	—	—	15·7 × 11·7	—	—
AM MF1093	—	—	16·6 × 10·8	—	—

TABLE 8

MAXILLARY MEASUREMENTS FOR *Protemnodon brehus* (OWEN)—BINGARA, N.S.W. SAMPLE

Specimen	M^2	M^3	M^4
AM F55356	—	16·7 × —	18·7 × 14·4
AM F55357	—	—	18·7 × 15·2
AM F55358	16·4 × 13·3	—	—
AM F55359	15·4 × 13·6	—	—
AM F55360	16·6 × 13·9	—	—
AM F55361	16·3 × 13·9	—	—

In addition to cranial specimens, Owen (1877) also referred a disassociated distal end of a left femur to *P. brehus*. Further post-cranial material, including the pelvis, fibula, astragalus, cuboid, navicular, cuneiforms and metatarsals are described for the species by Tedford (1967). There is no evidence to support the reference of the femur by Owen (1877) and as indicated previously, there is some possibility that there may be more than one species of *Protemnodon* represented in the cranial remains from the Lake Menindee deposits. Undoubtedly, the pes material referred by Tedford (1967) is of *Protemnodon* by comparison with the remains figured by Plane (1967) for *P. otibandus* from the Pliocene Awe Fauna, New Guinea, but the specific identification of the referred specimens while probably correct would best await verification of the presence of only one species of *Protemnodon* in the Lake Menindee area.

Two mandibular specimens, F3028 and F4942 in the Queensland Museum collections, although generally agreeing morphologically with the species, have not been able to be assigned conclusively to *P. brehus*. These specimens exhibit marked reduction in the breadth of the anterior cingulum, a feature not showing intergradation with the referred sample at this time.

P. brehus is separable from *P. anak* by a consideration of both size and morphology. Separation by size alone is not conclusive, as a degree of overlap for particular characters is encountered. Where more than one tooth is preserved in a specimen, additional checks can be made for overlap with *P. anak* and by this means the bulk of the sample may be defined. No single morphological feature is sufficient to diagnose *P. brehus* and as many characters as possible must be considered before assignment is made. Among the more important morphological features of use in the separation of *P. brehus* from *P. anak* are the much broader nature of P^3, the less concave nature of its labial surface, the broader extent of its lingual basin and the extension in the length of the lingual cingulum. The upper molars are morphologically similar but the anterior cingular shelf is more planar transversely. The mandibular symphysis is greatly elevated with respect to the base of the mandible while the labial groove is usually relatively closer to the alveolar margin. P_2 in *P. anak* is only slightly flexed lingually in the posterior extension of its longitudinal crest, while that in *P. brehus* is markedly flexed and approaches 90° in some specimens. In *P. brehus*, the trigonid basin in DP_3 is more planar transversely. As with the deciduous lower premolar, the longitudinal crest in P_3 is usually flexed to a greater extent than in *P. anak*, while the crown is broader posteriorly and more usually subtriangular than suboval in occlusal view. Lower molars are morphologically similar but the posterior cingulum tends to be more consistently better developed in *P. brehus*.

P. brehus is moderately widely distributed throughout Australia and apart from the records of the species in New South Wales already noted, the species is present from Cunningham Creek, County of Harden and from Lake Tandau in the lower Darling Region. Tedford (1967) indicates the presence of material compared with *P. brehus* at Curramulka, on Yorke Peninsula, and from the Warburton River, near Cowarie Station, in South Australia. Material from the Mammoth Cave in Western Australia also appears comparable with *P. brehus* (Tedford, 1967). The species is not yet recorded from Victoria and Tasmania.

Protemnodon roechus Owen, 1874

(Plates 16–19)

Protemnodon roechus Owen, 1873, p.128 (*nomen nudum*).

Protemnodon roechus Owen, 1874, p. 281, pl. 27, figs. 10–13; 1877, p. 434, pl. 87, figs. 10–13; Palmer, 1904, p. 883.

Protemnodon antaeus Owen, 1877, pp. 448–9, pl. 110, figs. 1–5; Etheridge Jnr., 1892, p. 766; Simpson, 1930, p. 76; Stirton, 1963, pp. 141–2, fig. 14b.

Macropus raechus (Owen): Lydekker, 1887, pp. 212–3; 1894, p. 257; 1896, p. 257.

Protemnodon raechus Owen: Etheridge Jnr., 1892, p. 678; Simpson, 1930, p. 76; Stirton, 1963, p. 142, fig. 15a.

MATERIAL: F3868, cast of holotype of *P. roechus* Owen, British Museum (Natural History) No. 35968, partial left mandibular ramus with P_3–M_3, adult, Gowrie, Darling Downs, (figd Owen, 1874, pl. 27, figs. 10–13; 1877, pl. 87, figs. 10–13).

F3397, cast of holotype of *P. antaeus* Owen, British Museum (Natural History) No. M2258, partial left mandibular ramus with P_3–M_4, adult, Queensland, (figd Owen, 1877, pl. 110, figs. 1–5).

Eleven juvenile mandibular rami, 39 adult mandibular rami, 6 isolated lower teeth, one nearly complete cranium, 2 premaxillae, 2 juvenile maxillae, one palate, 18 adult maxillae and 4 isolated upper teeth from the following localities in the eastern Darling Downs: King Creek; King Creek, Pilton; King Creek, Ravensthorpe, Upper Pilton; King Creek, Ravensthorpe, Pilton, at M.R. 190398 Liverpool Range 1 mile map; King Creek, at M.R. 045455 Clifton 1 mile map; King Creek, near M.R. 039454 Clifton 1 mile map; King Creek, at M.R. 134443 Liverpool Range 1 mile map; Clifton; King Creek, at M.R. 128445 Liverpool Range 1 mile map; Wellcamp, Darling Downs; Freestone Creek, Warwick; Gowrie Creek; Gowrie; Macalister; near Dalby; Condamine River, at M.R. 403644 Dalby 4 mile map; and from the eastern Darling Downs (particular localities unspecified).

Other Queensland localities represented include Russenden Caves, near Glen Lyon Caves, Pikes Creek, Texas area, SE.Q.; Knapp's Creek, near Beaudesert, at a depth of 40 feet in a well; near Roma, SE.Q.; and Lansdowne Station, near Tambo, C.Q.

SPECIFIC DIAGNOSIS: A large species, larger than *P. anak* and usually larger than *P. brehus*.

Mandible deep, with symphysis elongate, elevated to about 10° to base of mandible; lateral groove extends to below anterior root M_3, well below alveolar margin.

I_1 elongate, very deep, markedly curved in occlusal view; enamel flanged dorsolabially, but usually unflanged and rounded ventrolingually, tip wears to produce very rounded outline. P_2 relatively elongate, with longitudinal crest high, markedly concave lingually; crest transected by broad ill-defined ridges. DP_3 with lophids high; trigonid basin narrow with broad ridge descending anteriorly into basin from metaconid; anterolabial fossette absent; weak ridge descends anteriorly from entoconid; posterior cingulum usually absent or poorly defined. P_3 relatively elongate, high, often slightly constricted at posterior one-third; crest transected by one to three sets of broad vertical labial and lingual ridges; cuspules not well defined; anterior cuspid of crest almost above anterior tooth margin. Lower molars somewhat constricted, with high lophids; trigonid basin and anterior cingulum narrow; anterolingual fossette not developed; posterior

ridge from metaconid not developed; posterior cingulum usually absent with basal posterior crown surface broadly curved in lateral view.

Upper incisors extremely broadly U-shaped in occlusal outline; I^1 extremely large; I^3 relatively small. P^3 elongate, about as long as M^4; markedly concave labially with marked posterolabial flexure; longitudinal crest high, markedly concave labially; crest transected anteriorly by a major set of non-vertical ridges and posteriorly by one or two minor sets; minor cuspules present; lingual cingulum sometimes discontinuous, subparallel to crest, occasionally diverging anteriorly to above paracone; cingulum not markedly tuberculate in lingual aspect. Upper molars slightly constricted across valley, with high lophs; forelink generally absent; strong anterior ridge from paracone occasionally continues to limit of cingulum; relatively strong ridge ascends posteriorly from paracone towards midlink, while slight ridge ascends anteriorly from metacone into valley; lingual limit of valley usually with prominent tuberculation.

DESCRIPTION: Mandible moderately deep, relatively thick; base of symphysis elevated at approximately 10° to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit relatively deep, near posterior symphysial limit; diastema relatively elongate with crest posteriorly acute, more rounded anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen comparatively large, rounded, close to diastemal crest, about one-third distance along crest from P_3 to limit of ramus. Ramus with well defined, shallow, lateral groove extending posteriorly to below anterior root of M_3, frequently disrupted by roots of P_3; groove positioned about one-third distance from alveolar margin to base of ramus. Diagastric process separated from base of angle by very shallow post-diagastric sulcus, bounded above by shallow diagastric fossa; this fossa separated above from shallow depression opening posteriorly into larger pterygoid fossa. Post-alveolar shelf short, with shelf angle usually not well developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of alveolar margin; masseteric foramen moderately large, with masseteric fossa relatively deep. Angle of mandible markedly inflected, flexed posteriorly at margin, broadly rounded posteriorly, ascending at high angle to posterior limit of masseteric crest. Anterior margin of coronoid process reclining at slight angle to vertical; bulk of coronoid process and condyle not preserved in adult specimens.

I_1 elongate, deeply rooted, with crown deep in unworn and juvenile specimens, slightly curved in general lateral view, markedly curved in occlusal view, developing subhorizontal facet of wear with upper incisors, and mesial facet of wear at tip by approximation with other lower incisor; root compressed oval in section; crown subquadrantal in section, somewhat tapered anteriorly, enamelled laterally, this produced into dorsolabial flange, but usually broadly rounded ventrolingually; crown also enamelled ventromesially; distally, tip wears to produce very broadly rounded anterior margin.

P_2 relatively elongate, with labial and lingual surfaces near parallel in occlusal view, converging rapidly anteriorly. Longitudinal crest secant, somewhat curved posterolingually and anterolingually, giving crest a marked lingual concavity in occlusal view; crest

transected by only broad, vertical labial and lingual ridges; anterior cuspid of crest well defined, and posterior cuspid moderately well defined. Base of crown slightly tumid.

DP_3 molariform, subtriangular in basal outline, unconstricted or slightly constricted across talonid basin, with lophids moderately high, slightly convex posteriorly. Hypolophid much broader than protolophid. Trigonid basin narrow, its length being less than distance between lophids. Forelink moderately high, strong, curving anterolingually from protoconid to point somewhat labiad to axis of crown on relatively low anterior cingulum; broad ridge descends anteriorly from metaconid into trigonid; anterolabial fossette not developed in trigonid; lingual moiety of trigonid near planar, but labial moiety descends at high angle to crown margin. Midlink moderately high, strong, curving anterolingually from hypoconid across talonid basin to unite with short, posterior ridge from near midpoint of protolophid; weak ridge descends anteriorly from entoconid. Talonid basin sharply U-shaped, near planar, descending only slightly labially and lingually from midlink. Suggestion of posterior cingulum occasionally present but very poorly defined. Base of crown occasionally tumid, particularly at margins of talonid.

TABLE 9

MANDIBULAR MEASUREMENTS FOR *Protemnodon roechus* OWEN

Specimen	P_3	M_1	M_2	M_3	M_4
F3868 *	21·2 × 8·1	—	16·7 × —	20·0 × 12·8	—
F3397 **	18·8 × 6·5	13·1 × —	15·8 × —	17·9 × 11·9	20·0 × 12·3

* Cast of holotype *P. roechus*; ** Cast of holotype *P. antaeus*.

P_3 relatively elongate, high, morphologically simple, robust, deeply rooted; crown subovate to subtriangular in basal outline, but often very slightly constricted at posterior one-third; crest secant, moderately posterolingually curved; crest transected by one or occasionally two or three sets of broad, vertical, labial and lingual ridges, but usually without production of well defined, discrete cuspules at crest. Anterior cuspid of crest almost above anterior basal limit of crown, with anterior ridge from cuspid near vertical and straight in lateral view; anterior cuspid frequently strongly defined with longitudinal crest descending sharply from it posteriorly; posterior cuspid less well defined. Base of crown tumid.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, frequently somewhat constricted across talonid basin; lophids high, slightly convex posteriorly, with hypolophid broader than protolophid in M_1, approximately equal in M_2 and M_3, and slightly narrower in M_4. Trigonid basin narrow, its length approximately equalling distance between lophids. Forelink relatively high, strong, curving anterolingually from protoconid to near midpoint of low, narrow, very strongly developed anterior cingulum; this curves broadly from forelink to below protoconid, but is reduced anterolingually, and is more sharply curved lingually; trigonid basin descends at about same angle labially and lingually from forelink, but anterolingual fossette is not developed; very slight ridge descends anteriorly from metaconid, but posterior ridge into talonid basin is wanting. Midlink moderately high, strong, curving anterolingually from hypoconid to unite with

short ridge from near midpoint of protolophid, above talonid; midlink occasionally less strongly developed in posterior molars; slight ridge descends anterolabially from entoconid towards talonid; talonid basin sharply U-shaped, descending at moderate angle labially and lingually from midlink. Posterior cingulum usually absent. Base of crown usually extended posteriorly below hypolophid, frequently with basal swelling, this producing a broadly curved posterior crown surface. Lateral crown base, occasionally tumid, particularly at margin of talonid. Posterior base of crown usually marked by groove paralleling alveolar margin above limit of enamel, accompanied occasionally by minor vertical accessory ridges.

Cranium large, elongate with rostrum somewhat tapering anteriorly, only slightly deflected; maxillae dorsally in moderately wide contact with frontals; laterally with infraorbital foramen simple, above posterior of P^3 in adult specimens, positioned well in advance of jugal; infraorbital canal elongate but variable, being 39·1–43·0 (n = 3); inferior process of anterior zygoma root very strong, extending beyond level of occlusion of cheek teeth. Lacrymal expanded onto facial surface with lacrymal foramina on facial side of orbital rim; superior lacrymal tuberosity wide, bulbous with inferior tuberosity smaller. Premaxillae with anterior narial floor declining posteriorly, wide; anterior premaxillary narial spines very prominent; superior premaxillary surface extends posteriorly at low ascending angle, abruptly ascending above region of incisive foramen; labial foramen prominent, positioned towards margin of palate, well posterolateral to posterior rim of incisive foramen. Palate entire, penetrated posteriorly by anterior palatine foramen and posterior lateral foramen; palatines moderately large, extending anteriorly to about level of M^3 in adult specimens. Jugal laterally excavated for superficial layer of masseter, with zygomatic arches converging somewhat anteriorly, with zygomatic crest posteriorly curving backwards and ventrally. Roof of braincase arched with sagittal crest forming by confluence of ridges passing posteriorly from above orbits. Subsquamosal foramen separated below by continuation of zygomatic crest; squamosal widely separated from frontal, contributing with jugal, to glenoid fossa. External auditory meatus relatively low. Tympanic extending only slightly down paraoccipital process; processes not preserved, but bases strong. Basisphenoid only slightly grooved posteriorly at mid-line. Pterygoids slightly overlap basisphenoid, being in sutural contact. Supraoccipital relatively low, wide, with lambdoidal crest extending posteriorly to marked extent with well defined supraoccipital depressions separated by moderate, rounded, median nuchal crest; inferior supraoccipital depressions absent. Condyloid foramen prominent. Dorsal surface with nasal–frontal suture approximately level with anterior orbital rim. Nasals very retracted.

Upper incisors extremely broadly U-shaped in occlusal outline; I^1 extremely large compared with I^2 and I^3, axially curved; directed anteroventrally and somewhat mesially with tips approximated; labial surface curved towards occlusal surface but becoming grooved at posterior one-third towards limit of enamel; enamel surface extends anteromesially and posteromesially but does not reach lingual surface of crown; anterolateral, posterolateral and posteromesial margins of crown sharply rounded, but anteromesial margin broadly rounded; occlusal surface becomes nearly horizontal with wear, with slight projection of enamel where present, resulting in large area for occlusion. I^2 not

sufficiently well preserved to be described. I^3 relatively small, short in anteroposterior extent, not known in unworn condition; lateral surface marked by vertical groove about one-half way along its occlusal surface, this extending towards crown base; enamel present on all surfaces of crown; wear predominantly mesiad, with production of high angle wear facet ascending mesially.

No upper canine has yet been located, and P^2 and DP^3 are unknown.

P^3 elongate, being approximately as long as longest molar, slightly broader posteriorly than anteriorly; crown in occlusal view subcrescentic, markedly concave labially, with a marked posterolabial flexure, but nearly straight or slightly concave lingually; longitudinal crest secant, but also markedly posterolabially curved, moderately high; apex of paracone about one-fifth distance along crown from anterior point; anterior ridge from paracone frequently stronger, developed basally and curving lingually; crest transected anteriorly by major set of non-vertical labial and lingual ridges, and posteriorly by one or two minor sets of ridges; cuspules produced at crest, decreasing in development posteriorly. Hypocone moderately high, being about three-quarters as high as metacone, united to above metacone by strong, high, labial ridge; posterior ridge from metacone ascends towards crown base; posterior ridge from hypocone curves labially to above metacone; well defined posterior fossette developed between this and ridge connecting posterior cusps. Anterior ridge from hypocone ascends sharply to form low, frequently discontinuous anteriorly, lingual cingulum, generally subparalleling crest anteriorly, but occasionally slightly diverging anteriorly to above paracone, connected to it by moderately strong ridge. Ridges from cuspules along crest cross lingual basin to cingulum; anterolingual fossette occasionally formed particularly where cingulum discontinuous. In lingual aspect, cingulum not markedly tuberculate. Base of crown often markedly tumid.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, very slightly constricted across median valley; lophs moderately high, slightly bowed anteriorly; metaloph slightly broader than protoloph in M^1, approximately equal in M^2 and M^3 and somewhat narrower in M^4. Anterior cingulum low, relatively broad, short, nearly planar transversely; generally no trace of distinct forelink present, but occasional variable ridgelets pass from base of protoloph to cingulum; anterior margin of cingulum generally flattened. Moderately strong ridge ascends from paracone towards labial limit of cingulum, occasionally continued from base of protoloph across cingulum margin. Strong ridge usually ascends posterolingually from paracone towards midlink. Midlink moderately strong and high, curving posterolabially from protocone to unite with short ridge from near mid-point of metaloph, above median valley; relatively strong ridge curves posterolingually from paracone towards midlink; slight ridge from metacone ascends anterolingually into median valley. Median valley narrowly U-shaped labially, more broadly U-shaped lingually; base of valley near planar transversely; lingual limit of valley usually marked by prominent tuberculation. Strong, slightly flared ridge curves posterolabially from hypocone to base of crown slightly mesiad to posterolabial limit, uniting with weaker ridge ascending slightly posterolingually from metacone. Slight posterior fossette formed between ridges and base of metaloph, labiad to crown axis.

DISCUSSION: Material referred to *Protemnodon roechus* Owen is moderately common in the Pleistocene fluviatile deposits of the Darling Downs and is recorded from isolated

TABLE 10

SUMMARY OF MEASUREMENTS FOR *Protemnodon roechus* OWEN

Character	Maxillae					Mandibles				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
I_1 depth	—	—	—	—	—	2	17·9–18·2	18·1	—	—
P_2 length	—	—	—	—	—	2	11·9	11·9	—	—
Maximum breadth	—	—	—	—	—	2	6·2– 6·3	6·3	—	—
DP_3 length	—	—	—	—	—	3	11·6–11·9	11·7	0·1599	1·37
Breadth protolophid	—	—	—	—	—	3	6·8– 7·4	7·2	0·3240	4·50
P^3_3 length	7	18·3–20·7	19·4	0·7538	3·89	11	17·5–21·2	18·8	0·9121	4·85
Maximum breadth	7	9·2–10·4	9·7	0·4337	4·47	13	6·0– 8·1	7·0	0·5852	8·36
M^1_1 length	4	12·9–14·0	13·4	0·5567	4·15	12	12·4–14·2	13·3	0·6612	4·97
Breadth protoloph (-id)	9	12·2–13·9	12·8	0·5926	4·63	8	8·9– 9·9	9·4	0·3761	4·00
M^2_2 length	12	15·7–17·7	16·7	0·6037	3·61	22	14·0–18·0	16·1	0·9332	5·80
Breadth protoloph (-id)	10	13·7–15·4	14·6	0·5217	3·57	11	10·6–12·2	11·3	0·5147	4·55
Height*	2	12·2–12·5	12·4	—	—	1	10·5	—	—	—
M^3_3 length	18	17·2–19·9	18·6	0·8311	4·47	28	16·8–20·3	18·5	0·9704	5·25
Breadth protoloph (-id)	12	14·9–16·2	15·6	0·3512	2·25	31	11·2–13·6	12·5	0·5193	4·15
Height*	3	12·4–13·2	12·8	—	—	10	7·9–10·6	9·7	0·7370	7·60
M^4_4 length	13	17·7–20·0	19·0	0·7900	4·16	24	17·3–20·9	19·7	0·6896	3·50
Breadth protoloph (-id)	11	14·7–16·5	15·7	0·5531	3·52	22	11·1–13·8	12·6	0·6015	4·77
Height*	7	9·9–13·1	11·5	1·1075	9·63	13	8·3–10·0	9·2	0·5074	5·52

* Enamel height measured at hypocone and entoconid in unworn teeth.

localities from other parts of Queensland, but it is not nearly as well represented in collections as the smaller species, *P. anak*. The species was described by Owen (1874) and includes the largest representatives of the genus yet known. Slightly smaller representatives, previously referred to the species *P. antaeus*, described by Owen (1877), cannot be separated from *P. roechus* by either size or structure where the sample is sufficiently large for variation to be taken into account. The holotype of *P. antaeus* is morphologically very similar to *P. roechus* and the two are here regarded as synonymous. Measurements for the holotype specimens are presented in Table 9.

Association of upper and lower dentigenous fragments of *P. roechus* has been achieved through a combined consideration of both size and morphology. No attempt has been made to associate any of the post-cranial material in the Queensland Museum collections with the described cranial remains because of the disarticulated and fragmentary nature of the specimens at present known.

The accompanying summary of measurements, Table 10, presents statistical evaluation of the population of *P. roechus* represented in the holdings of the Queensland Museum and includes both mandibular and maxillary specimens. The generally low values for the Coefficient of Variation are in keeping with values for other species of *Protemnodon* here considered and with other fossil and recent macropodids (Bartholomai, 1971). As with other species of *Protemnodon* values for V for height of enamel are moderately high compared with other characters considered and for reasons presented for other species, discussed above, are not indicative of real variation in the height of the crown. The sample of *P. roechus* presents only very limited numbers of specimens possessing certain of the characters considered and, in these cases, the statistical results represent no more than a guide to the range of variation exhibited in the local population.

An indication of the variation present in the premolar teeth is illustrated in Figure 7, while measurements for the referred upper incisor teeth are shown in Table 11.

P. roechus is distinguished from other known species of *Protemnodon* by both its extreme size and generally distinct morphology. In particular, the relatively less ornamented nature of its permanent lower premolar, the broadly rounded, swollen condition of the posterior crown bases of the lower molars, the non-vertical transecting ridges of the permanent upper premolars, the crescentic shape of this tooth in occlusal view and the generally marked tuberculation of the lingual extremity of the median valley in upper molars are all useful in the morphological separation of the species. Overlap in size does occur with *P. brehus*, but by applying a combination of the characters available, separation of the species is achieved.

Several mandibular specimens from the Pleistocene fluviatile deposits are present whose taxonomic position has not been able to be satisfactorily resolved and these are referred doubtfully to the present species, but have not been considered statistically in this study. These include F5082 and F3039, both of which are within the size range of *P. roechus* and have generally similar morphology to the referred material, but have a well developed posterior cingulum. F5084, also included in this doubtfully referred material, is morphologically identical to *P. roechus* but is much smaller, within the size range of *P. anak* specimens.

A very small sample of mandibular remains of *P. roechus* derived from the Pleistocene fluviatile deposits at Bingara, New South Wales, is present in material made available from the Australian Museum, Sydney. Variation in this sample is entirely encompassed by that seen in the Darling Downs material. Measurements for the Bingara sample are presented in Table 12.

TABLE 11

MEASUREMENTS FOR UPPER INCISORS IN *Protemnodon roechus* OWEN

Specimen	F5053	F5295	F5284	F5294	F5291
Length I^1 ..	16·1	17·0	15·3	14·8*	15·2
Length I^3 ..	8·0*	—	—	—	—

* Estimated

Apart from the localities already noted, *P. roechus* has not been as widely mentioned in literature as other Pleistocene species. Tindale (1933) has recorded it from the Tantanoola Caves in the southeast of South Australia but the record is not accompanied by either a description or figure and the identity of the specimen must at present remain in doubt. Specimens exist in the Australian Museum, Sydney, which are undoubtedly of *P. roechus* and which were derived from the Wellington Caves. Within these, there is a tendency towards narrowing of the anterior cingulum and trigonid basin, an extreme of which is present in AM F30524, a right ramus with M_2–M_4 preserved.

TABLE 12

MANDIBULAR MEASUREMENTS FOR *Protemnodon roechus* OWEN—BINGARA SAMPLE

Specimen	M_2	M_3	M_4
AM MF1233 ..	—	18·0 × 12·0	19·0 × 12·1
AM MF1221 ..	—	—	19·7 × 13·2
AM MF1157 ..	16·1 × —	17·9 × 12·1	19·4 × 12·6

Protemnodon chinchillaensis sp. nov.

(Plates 20–21)

Protemnodon anak Owen: De Vis. 1895 (*partim*), pp. 104–109.

MATERIAL: F5246, holotype, partial right mandibular ramus with M_2–M_4, adult, Chinchilla Sand of late Pliocene age, Chinchilla, SE.Q. This specimen has been associated with the anterior portion of a right mandibular ramus with P_3, previously numbered F5238.

Eight juvenile mandibular rami, 19 adult mandibular rami, 1 isolated lower tooth, 2 juvenile maxillae, 11 adult maxillae and 5 isolated upper teeth from the following localities in the Chinchilla Sand, in the western Darling Downs: Chinchilla, SE.Q.; Middle Gully System, Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla), 55 feet above low water level; and from the western Darling Downs (particular localities unspecified).

SPECIFIC DIAGNOSIS: A small species, generally somewhat smaller than *P. anak*.

Mandible comparatively very shallow, with symphysis relatively elongate, ascending at about 5° to base of mandible; lateral groove extends posteriorly to below anterior root M_3, well below alveolar margin; mental foramen close to anterior root P_3.

P_2 elongate, relatively low crowned, with crest slightly curved lingually in its posterior extension; crest transected by two or three sets of vertical labial and lingual ridges; cuspules present. DP_3 slightly constricted across talonid basin, with low lophids; protolophid very convex posteriorly; trigonid basin relatively narrow; forelink slightly curved; strong, angular ridge descends from metaconid to lingual limit of high anterior cingulum, across swollen base of protolophid; anterolabial fossette present; lingual moiety of trigonid pocket-like; midlink relatively strong; weak ridges from metaconid and entoconid unite across talonid; posterior cingulum well defined. P_3 very elongate, much longer than M_4, constricted at posterior one-third; crest low, usually straight, transected by four or five sets of vertical labial and lingual ridges; cuspules present. Lower molars slightly to markedly constricted across talonid basin, with lophids low, forelink labiad to midline; slight ridge descends anteriorly from metaconid; base of protolophid swollen lingually; midlink labiad to mid-line; slight ridges from metaconid and entoconid often unite across talonid, close to midlink, talonid broadly U-shaped; posterior cingulum usually well defined, broad.

DP^3 with midlink paralleled labially by low ridge across valley. P^3 very elongate, much longer than M^4, with longitudinal crest low, nearly straight; crest transected by four or five sets of vertical labial and lingual ridges, cuspules present; lingual cingulum often continues anteriorly to near anterior of crown base; cingulum markedly sinuous and tuberculate in lingual view. Upper molars with low lophs, unconstricted or slightly constricted across valley of anterior molars but more constricted posteriorly; strong, high, ridge usually ascends from paracone to limit of cingulum, but this sometimes reduced in M^4; midlink relatively low; strong ridges from paracone and metacone normally unite across median valley giving impression of additional low link.

DESCRIPTION: Mandible very shallow, relatively thick; base of symphysis ascending anteriorly at an angle of approximately 5° to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit relatively shallow, near posterior symphysial limit; diastema elongate, with diastemal crest broadly angular posteriorly, more rounded anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen small, oval, near diastemal crest, close to anterior root P_3. Ramus with moderately deep lateral groove extending posteriorly to below anterior root M_3, usually somewhat disrupted by roots of P_3; groove positioned well below alveolar margin, about one-third depth of ramus below alveolar margin. Diagastric process separated from base of angle by very shallow post-diagastric sulcus, bounded above by shallow diagastric fossa; this fossa separated above from shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf moderately short, with well defined shelf angle usually not developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of alveolar margin; masseteric

foramen moderately large, with deep masseteric fossa. Angle of mandible, bulk of coronoid process and condyle not preserved.

I_1 not preserved.

P_2 relatively elongate, subovate in occlusal view, with lingual surface slightly convex and labial surface markedly convex. Longitudinal crest secant, slightly curving lingually in its posterior extension; anterior ridge from anterior cuspid slightly curved lingually and strengthening towards base of crown; crest transected by two or three sets of vertical labial and lingual ridges, with production of cuspules at crest; ridges and cuspules progressively weaken posteriorly; anterior cuspid of crest well defined, but posterior cuspid less well developed. Base of crown somewhat tumid.

DP_3 molariform, subtriangular in basal outline, slightly constricted across talonid basin, with lophids relatively low, with hypolophid slightly convex posteriorly and with protolophid very convex posteriorly; hypolophid much broader than protolophid. Trigonid basin relatively narrow, its length being less than distance between lophids. Forelink moderately high, strong, very slightly curving anterolingually or straight from protoconid to near midpoint of moderately high anterior cingulum; strong angular ridge descends anteriorly from metaconid to lingual limit of anterior cingulum, across swollen base of protolophid; labially, cingulum unites with protolophid base with production of slight anterolabial fossette; lingual portion of trigonid base pocket-like, near horizontal, but labial moiety descends at high angle. Midlink relatively strong, curving anterolingually from hypocone across talonid basin to unite with slight ridge from near midpoint of protolophid; weak ridge descends posteriorly from metaconid across lingual moiety of talonid to unite with weak anterior ridge from entoconid. Talonid basin sharply U-shaped, descending at greater angle labially than lingually from midlink. Posterior cingulum well defined, near horizontal with very slight ridge ascending at posterolingual margin of crown to entoconid. Base of crown slightly tumid, particularly at labial extremity of talonid basin.

P_3 comparatively very elongate, robust, deeply rooted; crown subovate to dumbell shaped in basal outline, slightly to strongly constricted at posterior one-third, with longitudinal crest secant, straight or very slightly concave lingually except for lingual flexure in its posterior extension; crest usually transected by five sets of vertical labial and lingual ridges with production of cuspules at crest, but occasionally four sets of ridges and resultant cuspules present; strength of ridges and cuspules decreases posteriorly; anterior cuspid of crest well defined, but posterior cuspid less well developed; base of crown slightly tumid.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly to markedly constricted across talonid basin; lophids relatively low, slightly convex posteriorly, with hypolophid broader than protolophid in M_1, approximately equal in M_2 and M_3 and narrower in M_4. Trigonid basin relatively broad, its length approximately equalling distance between lophids. Forelink moderately low, relatively strong, curving anterolingually from protoconid across trigonid to point on anterior cingulum labiad to midline. Anterior cingulum low, generally broadly curved anteriorly, near horizontal lingually but descending slightly labially; slight ridge descends anteriorly from metaconid; base of protolophid swollen in lingual moiety, very occasionally with suggestion of presence of

accessory vertical ridge. Midlink moderately low, moderately strong but usually decreasing in strength in posterior molars, curving anterolingually from hypoconid to unite with slight ridge from protolophid from point labiad to midline; slight ridge descends posterolabially from metaconid and frequently unites across talonid, close to midlink, with slight anterolabial ridge from entoconid. Talonid basin broadly U-shaped, descending at low angle labially and lingually from midlink; occasionally, labial moiety ornamented with low, transverse ridge. Posterior cingulum usually well defined, frequently extending across entire posterior of crown, occasionally united by slight ridge to entoconid.

Cranium known only from fragmentary maxillary remains.

Upper incisors unknown, and P^2 known only in very fragmentary state.

DP^3 preserved only in worn and partially shattered condition; molariform, subrectangular in basal outline, with low lophs; paracone not preserved; anterior cingulum connected to base of protoloph by slight ridges near axis of crown; midlink moderately strong, paralleled labially by low ridge across median valley uniting paracone and metacone. Strong ridge curves posterolabially from hypocone to above metacone; weaker ridge ascends slightly lingually from metacone to unite with this, defining posterior margin to posterior fossette.

P^3 relatively very elongate, being much longer than any molar, somewhat broader posteriorly than anteriorly; crown with longitudinal crest secant, relatively low, usually nearly straight except in posterior extension where crest is slightly labially flexed; apex of paracone about one-fifth distance along crown from anterior limit; crest transected by five or sometimes four sets of vertical labial and lingual ridges, with production of cuspules at crest; strength of ridges and cuspules decreases posteriorly. Hypocone moderately high, being about three-quarters as high as metacone, united to above metacone by strong, high, labial ridge; strong ridge from hypocone ascends posterolabially to unite with posterior ridge from metacone; well defined posterior fossette developed between this and ridge connecting posterior cusps. Anterior ridge from hypocone ascends sharply to form low lingual cingulum, generally converging anteriorly to above paracone, connected to it by moderately strong vertical ridge; slight extension of lingual cingulum occasionally ascends beyond this point to anterolingual base of crown; more prominent ridges from cuspules along longitudinal crest cross shallow lingual basin to lingual cingulum; cingulum markedly sinuous and tuberculate in lingual aspect. Base of crown somewhat tumid.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, unconstricted or slightly constricted across median valley in anterior molars, frequently more so in M^4; lophs relatively low, slightly bowed anteriorly, with metaloph broader than protoloph in M^1, approximately equal in M^2, slightly narrower in M^3 and usually markedly narrower in M^4. Anterior cingulum low, broad and short, slightly descending labially; generally no trace of a distinct forelink present; variable slight ridges usually pass from base of protoloph towards cingulum; cingulum generally broadly rounded anteriorly. Strong, high ridge ascends anteriorly from paracone to labial limit of cingulum, but this is sometimes reduced in M^4. Midlink relatively low, usually moderately strong in anterior molars but quite weak in some posterior molars, curving posterolabially from protocone to unite with slight ridge from near midpoint of metaloph, above median valley; in anterior

TABLE 13

SUMMARY OF MEASUREMENTS FOR *Protemnodon chinchillaensis* SP. NOV.

Character	Maxillae					Mandibles				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
P_2 length	—	—	—	—	—	2	9·6–11·1	10·4	—	—
Maximum breadth	—	—	—	—	—	2	4·5– 5·5	5·0	—	—
DP^3_3 length	2	10·2–10·7	10·5	—	—	4	9·6– 9·9	9·7	0·1288	1·33
Breadth protolophid	—	—	—	—	—	4	5·7– 6·4	6·0	0·3414	5·69
P^3_3 length	1	19·5	19·5	—	—	9	15·7–17·9	17·1	0·6117	3·58
Maximum breadth	4	8·2– 9·2	8·7	0·4242	4·88	9	4·9– 6·2	5·5	0·3674	6·68
M^1_1 length	4	10·4–11·6	11·0	0·4967	4·52	8	9·9–11·4	10·6	0·6939	6·55
Breadth protoloph (-id)	5	9·3–11·3	10·3	0·7314	7·10	7	7·8– 8·3	8·0	0·1958	2·45
M^2_2 length	7	11·7–13·4	12·5	0·5400	4·32	15	10·9–12·8	12·1	0·5977	4·94
Breadth protoloph (-id)	9	10·5–12·6	11·7	0·6072	5·19	15	8·6– 9·5	9·1	0·2718	2·99
Height*	2	8·1–10·4	9·3	—	—	6	6·4– 7·4	6·8	0·3847	5·66
M^3_3 length	6	13·3–14·7	14·2	0·5603	3·95	15	12·7–14·8	13·6	0·5856	4·31
Breadth protoloph (-id)	6	11·6–12·9	12·3	0·5933	4·82	15	9·5–10·9	9·9	0·3769	3·81
Height*	3	7·3– 8·8	7·9	—	—	9	6·3– 7·7	6·9	0·4885	7·08
M^4_4 length	12	13·7–14·8	14·3	0·4400	3·08	8	13·5–14·6	14·1	0·4140	2·94
Breadth protoloph (-id)	11	10·7–13·0	12·1	0·7183	5·94	8	9·2–10·1	9·7	0·3184	3·28
Height*	11	6·6– 9·0	7·7	0·5857	7·61	7	6·0– 7·5	6·6	0·4812	7·29

* Enamel height measured at hypocone and entoconid in unworn teeth.

TABLE 14

MANDIBULAR MEASUREMENTS FOR *Protemnodon chinchillaensis* SP. NOV.

Specimen	P_3	M_1	M_2	M_3	M_4
F5246 * ..	17·6 × 5·9	—	10·9 × 8·8	13·5 × 9·8	14·6 × 9·2

* Holotype *P. chinchillaensis*

molars and to some extent in posterior molars, strong ridge ascends posterolingually from paracone usually to unite with equally strong ridge ascending anterolingually from metacone across median valley about one-half way between midlink and labial margin; this frequently gives crown the appearance of possessing lateral links. Median valley narrowly V-shaped labially and lingually; base of valley not markedly ascending labially or lingually from midlink. Strong, slightly flared ridge ascends posterolabially from hypocone to posterolabial base of crown, uniting with lesser ridge from metacone; this delimits posterior fossette slightly labiad to crown axis.

DISCUSSION: Most of the material here referred to *P. chinchillaensis* sp. nov. was included in that referred by De Vis (1895) to *Halmaturus anak*. De Vis's (1895) concept of the specific limits within the genus was extremely broad, and he stated that he could not determine any criteria by which separation could be achieved. It was, however, acknowledged that the variation exhibited by the combined sample was high.

It has now been widely illustrated that an age difference occurs within the Darling Downs samples, and that this is frequently indicated by specific and even generic differences between material from the Pleistocene fluviatile deposits and that from the Chinchilla Sand (Bartholomai, 1972).

P. chinchillaensis is the smallest species of *Protemnodon* yet recorded from Australia, and is morphologically distinct from other Pliocene and Pleistocene species. It is slightly larger than the small Pliocene New Guinea species, *P. buloloensis* Plane. Major morphological features distinguishing it from species from the Pleistocene fluviatile deposits include the low crown heights of the cheek teeth, the relatively more elongate permanent premolars compared with molar lengths, the relative strength of molar accessory ridging and the moderately weak midlinks, and the shallow depth of the mandibular ramus.

Its distinction from the other Chinchilla Sand species, *P. devisi* sp. nov. described below, is by both size and morphology. In particular, *P. chinchillaensis* is smaller, and has the mandibular ramus shallower, while the permanent premolars are comparatively longer, the links are more curved in the molars, and the anterolingual base of the protolophid is swollen. The comparatively more elongate nature of the permanent lower premolar also serves to separate *P. chinchillaensis* from *P. buloloensis*.

As seen in the accompanying summary of maxillary and mandibular measurements, outlined in Table 13, the sample is not large, and many of the characters are too inadequately represented to allow all but the broadest generalities on the population to be drawn. Values for the Coefficient of Variation are comparable with those for other species of *Protemnodon*, and are generally not excessive. The occasional, extremely low values for V are believed to relate to the small size of the sample. Measurements for the holotype

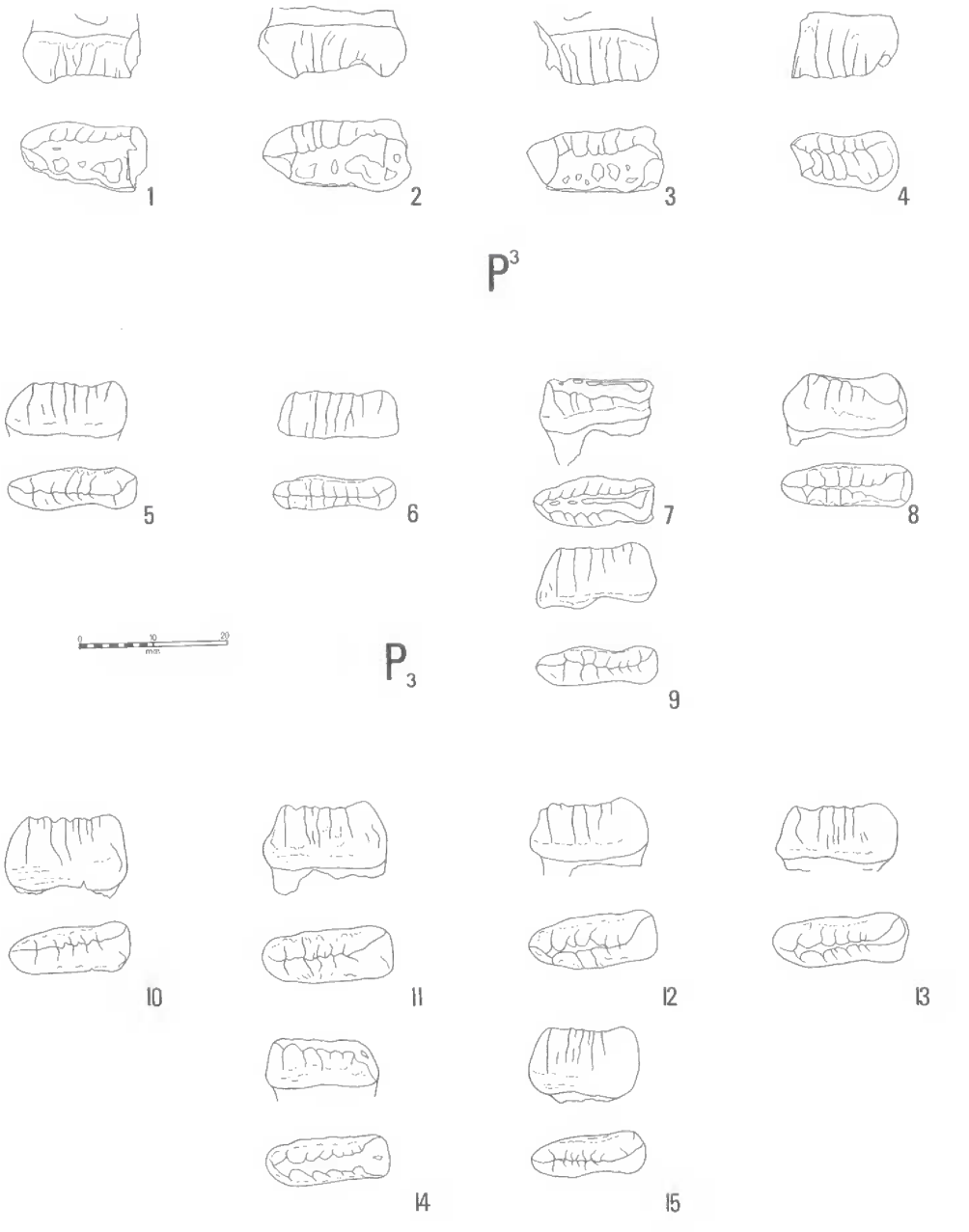

FIG. 8: Morphological variation in the permanent premolar teeth in *Protemnodon chinchillaensis* sp. nov. (1–9) and *Protemnodon devisi* sp. nov. (10–15). Lateral view above, occlusal view below. 1, right P^3 reversed, F5244; 2, left P^3, F4719; 3, right P^3 reversed, F4727; 4, right P^3 reversed, F5243; 5, left P_3, F3676; 6, left P_3, F5242; 7, left P_3, F5299; 8, right P_3 reversed, F5246; 9, right P_3 reversed, F4813; 10, right P_3 reversed, F4720; 11, right P_3 reversed, F3042; 12, left P_3, F4709; 13, left P_3, F4664; 14, left P_3, F4710; 15, left P_3, F4807.

specimen, F5246, are listed in Table 14, while variation in morphology in premolar teeth is illustrated in Figure 8.

General morphological resemblances of the species are with *P. anak* rather than with any other of the Pleistocene species, but at this stage too little is known of *P. chinchillaensis* for any definite relationships to be suggested.

Protemnodon devisi sp. nov.

(Plates 22–3)

Protemnodon anak Owen: De Vis, 1895 (*partim*), pp. 104–109.

MATERIAL: F4710, holotype, partial left mandibular ramus with P_3, M_2–M_4, adult, Chinchilla Sand of late Pliocene age, Chinchilla, SE.Q. This specimen has been reassociated with the anterior portion of a left mandibular ramus with P_3, previously numbered F4671.

Nine juvenile mandibular rami, 35 adult mandibular rami, 5 isolated lower teeth, 2 juvenile maxillae, 9 adult maxillae and 4 isolated upper teeth, from the following localities in the late Pliocene Chinchilla Sand, in the western Darling Downs: Chinchilla, SE.Q.; near Condamine River, gully in eastern part of por. 270, Par. Chinchilla; ?Chinchilla; near M.R. 362676 Chinchilla 4 mile map; well at Ehlma Siding, about 60′ below surface; and from the western Darling Downs (particular localities unspecified).

SPECIFIC DIAGNOSIS: A medium-sized *Protemnodon*, generally somewhat larger than *P. anak*.

Mandible moderately shallow, with symphysis elongate, elevated at about 15° to base of mandible; lateral groove extends posteriorly to below M_2–M_3.

P_2 relatively elongate, with crest low, slightly convex labially, transected by two sets of vertical labial and lingual ridges; cuspules present. DP_3 unconstricted across talonid, with lophids low; forelink labiad to axis of crown; anterolabial fossette present in trigonid; midlink labiad to axis; moderate ridge descends anteriorly from entoconid into talonid; broad, well defined posterior cingulum present. P_3 relatively elongate, with longitudinal crest moderately high, crown somewhat constricted at posterior one-third; crest nearly straight, transected by three or four sets of vertical labial and lingual ridges; cuspules present. Lower molars slightly constricted across talonid, with lophids low; trigonid very broad, near planar transversely; anterolabial fossette slight; forelink only slightly curved, as is midlink; midlink relatively low; slight ridge occasionally descends anteriorly from entoconid into talonid; posterior cingulum broad.

P^2 elongate, considerably broader posteriorly than anteriorly; lingual crest moderately low, slightly concave labially, transected by two sets of vertical labial and lingual ridges; cuspules present; third lingual ridge present posteriorly; lingual cingulum continues to above paracone; cingulum sinuous and tuberculate in lingual view. DP^3 slightly constricted across median valley; lophs low; anterior cingulum broad; strong ridge ascends from paracone to labial limit of cingulum; midlink relatively low, only slightly curved; relatively strong ridges from paracone and metacone unite across median valley. P^3 elongate, with longitudinal crest low, nearly straight; crest transected by four sets of vertical labial and lingual ridges; cuspules present; lingual cingulum continues anteriorly to near anterior crown limit; cingulum very irregularly sinuous in lingual view. Upper

TABLE 15

SUMMARY OF MEASUREMENTS FOR *Protemnodon devisi* SP. NOV.

Character	Maxilla					Mandible				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
P_2^2 length	1	13·8	13·8	—	—	2	9·6–10·4	10·0	—	—
Maximum breadth	1	7·9	7·9	—	—	2	5·0– 5·3	5·2	—	—
DP_3^3 length	1	12·0	12·0	—	—	2	9·7– 9·8	9·8	—	—
Breadth protoloph (-id)	1	9·4	9·4	—	—	2	5·7– 6·0	5·9	—	—
P_3^3 length	2	19·4–19·6	19·5	—	—	9	15·8–17·5	16·7	0·6633	3·97
Maximum breadth	2	9·3–10·4	9·8	—	—	12	5·5– 7·5	6·5	0·6522	10·03
M_1^1 length	4	12·2–13·2	12·6	0·4202	3·33	8	10·8–12·2	11·5	0·4225	3·67
Breadth protoloph (-id)	4	10·4–12·0	11·4	0·7164	6·28	9	7·9– 8·9	8·4	0·3201	3·81
M_2^2 length	7	13·7–15·6	14·6	0·7234	4·95	22	11·8–15·5	13·9	0·8978	6·46
Breadth protoloph (-id)	6	12·5–13·8	13·2	0·4604	3·49	21	9·1–11·1	10·0	0·4577	4·58
Height*	4	8·9–11·7	10·8	1·2832	11·88	10	6·3– 8·2	7·6	0·6624	8·72
M_3^3 length	8	14·3–16·6	15·7	0·7679	4·89	23	14·8–16·9	15·9	0·4981	3·13
Breadth protoloph (-id)	8	12·5–14·0	13·2	0·5428	4·11	24	10·3–12·0	11·3	0·4759	4·21
Height*	4	11·0–11·8	11·5	0·3558	3·09	9	6·7– 8·7	7·7	0·6412	8·33
M_4^4 length	3	16·2–17·1	16·5	—	—	14	15·5–17·9	16·5	0·6462	3·92
Breadth protoloph (-id)	3	13·4–13·8	13·6	—	—	17	10·5–12·0	11·2	0·5055	4·51
Height*	2	8·2–10·1	9·2	—	—	7	6·4– 8·6	7·3	0·7659	10·49

* Enamel height measured at hypocone and entoconid in unworn teeth.

molars very slightly constricted across median valley, with lophs low; relatively strong ridge ascends from paracone to labial limit of cingulum; midlink moderately low, very slightly curved; strong ridge from metacone across median valley; lingual limit of valley occasionally tuberculate.

DESCRIPTION: Mandible relatively shallow and thick; base of symphysis elevated at approximately 15° to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit relatively deep, near posterior symphysial limit; diastema relatively elongate with crest posteriorly acute, becoming more broadly rounded anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen relatively large, rounded, usually well below diastemal crest but sometimes close to crest. Ramus with well defined, shallow, lateral groove extending posteriorly to below M_2–M_3, often disrupted by roots of P_3; groove positioned about one-third distance from alveolar margin to base of ramus. Diagastric process bounded above by diagastric fossa; this fossa separated above from very shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, with shelf angle usually not well developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process. Coronoid process, condyle and angle of mandible not preserved in any specimen.

I_1 not preserved.

P_2 relatively elongate, very slightly broader posteriorly than anteriorly. Longitudinal crest secant, slightly convex labially, more flexed lingually in its posterior extension; slight fossette formed posterior to posterior cuspid. Crest transected by two sets of vertical labial and lingual ridges with production of cuspules at crest; strength of ridges and cuspules decreases posteriorly. Anterior cuspid of crest well defined. Base of crown tumid.

DP_3 molariform, subtriangular in occlusal view, unconstricted across talonid basin, with protolophid much narrower than hypolophid. Trigonid basin very broad, elongate. Forelink well defined, extending anteriorly to point on anterior cingulum labiad to axis of crown; anterior cingulum relatively low; slight fossette present in labial moiety of trigonid. Midlink moderately strong, curving anterolingually from hypoconid to point on protolophid labiad to crown axis; talonid basin shallowly U-shaped in labial and lingual moieties; moderate ridge descends anterolabially from entoconid across talonid about one-half way between midlink and lingual margin; labially, talonid margin somewhat tumid. Moderate ridge descends posteriorly from entoconid to unite with lingual limit of broad, well defined posterior cingulum, nearly as broad as posterior base of hypolophid.

P_3 relatively elongate, moderately high, robust, deeply rooted; crown subovate in occlusal view, usually broadest mesially, somewhat constricted basally at posterior one-third. Crest secant, nearly straight, usually being only very slightly convex labially; posterior extension slightly more flexed lingually; crest transected by three and sometimes four sets of vertical labial and lingual ridges with production of cuspules at crest; strength of ridges and cuspules decreases posteriorly. Anterior ridge from anterior cuspid descends at moderate angle to crown base. Base of crown slightly tumid.

TABLE 16

MANDIBULAR MEASUREMENTS FOR *Protemnodon devisi* SP. NOV.

Specimen	P_3	M_1	M_2	M_3	M_4
F4710 * ..	— × 5·8	—	—	15·1 × 10·5	15·6 × 10·6
AM F15464	—	—	14·0 × 10·5	16·0 × 11·5	16·8 × 11·4

* Holotype *P. devisi* sp. nov.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly constricted across talonid basin; lophids relatively low, slightly convex posteriorly, with hypolophid broader than protolophid in M_1 and M_2, approximately equal in M_3 and somewhat narrower in M_4. Trigonid basin very broad, elongate, its length approximately equalling distance between lophids. Forelink relatively high, moderately strong, slightly curving anterolingually from protoconid to near midpoint of low, very broad, anterior cingulum; cingulum broadly curved labially and lingually from forelink to base of protolophid; trigonid basin near planar transversely, often with slight anterolabial fossette formed at margin of labial moiety; anterior ridge from metaconid usually absent, often replaced by slight groove. Midlink relatively weak, moderately low, slightly curving anterolingually from hypoconid to point labiad to crown axis on protolophid; very slight ridge occasionally present descending anterolabially from entoconid towards talonid basin; basin sharply U-shaped labially and lingually, descending at approximately same angle from midlink, in both moieties. Slight posterior ridge from entoconid descends to unite with lingual extremity of posterior cingulum; occasionally, slight ridge also present from hypoconid, descending to labial margin of cingulum; cingulum broad, well defined.

Cranium known only from extremely fragmentary maxillary remains.

Upper incisors unknown.

P^2 elongate, robust, subtriangular in basal outline, considerably broader posteriorly than anteriorly; longitudinal crest moderately low, secant, slightly concave labially; crest transected by two sets of vertical labial and lingual ridges with production of cuspules at crest; posteriorly, a third lingual ridge descends to crest; apex of paracone positioned about one-quarter length of crown from anterior limit. Hypocone moderately strong, united to metacone by strong, high, descending anterolabial ridge; posterior ridge from hypocone curves labially, ascending slightly towards crown base above metacone, uniting with posterior extension of longitudinal crest from metacone; well defined posterior fossette formed between this and ridge connecting cusps; anterior ridge from hypocone ascends rapidly to above crown base to form low lingual cingulum, converging markedly anteriorly to above paracone; paracone connected to cingulum by moderately strong lingual ridge; cingulum in lingual view markedly sinuous, tuberculate. Lingual basin shallow, subdivided into well defined pockets by extensions of ridges from cuspules at longitudinal crest to cingulum. Base of crown slightly tumid labially and anterolingually.

DP_3 molariform, subtriangular in basal outline, slightly constricted across median valley. Lophs moderately low, slightly convex anteriorly, with metaloph broader than protoloph. Anterior cingulum low, broad, short, near planar transversely; several

moderately strong ridgelets pass from base of protoloph to anterior cingulum, but distinct forelink not developed; cingulum flattened anteriorly, with strong ridge descending from labial margin to paracone; slight anterolingual fossette present at lingual limit of cingulum. Midlink relatively strong, moderately low, slightly curving posterolabially from protocone to unite with slight ridge from near midpoint of metaloph; relatively strong ridge curves posterolingually from paracone to unite with similar ridge from metacone across median valley, about one-half way between midlink and labial margin. Median valley sharply U-shaped, near planar transversely. Strong, slightly flared ridge curves posterolabially from hypocone to above metacone, uniting with lesser ridge from that cusp. Posterior fossette delimited by these ridges, positioned slightly labiad to crown axis.

P^3 elongate, subtriangular in basal outline, somewhat broader posteriorly than anteriorly; crown in occlusal view very slightly concave labially, generally anteriorly converging lingually; longitudinal crest secant, nearly straight, relatively low. Apex of paracone about one-fifth distance along crown from anterior point; crest transected by four sets of vertical labial and lingual ridges with production of cuspules at crest; ridges and cuspules decrease in strength posteriorly. Hypocone moderately strong, connected to metacone by strong, high, labial ridge; posterior ridge from metacone ascends towards crown base; posterior ridge from hypocone curves labially; well defined posterior fossette developed posterior to ridge connecting posterior cusps; anterior ridge from hypocone ascends rapidly to above crown base, then continues anteriorly as low lingual cingulum; ridge from cingulum to paracone not always developed and cingulum continues anteriorly to point slightly linguad to anterior margin of crown; lingual basin shallow, crossed by extensions of ridges from cuspules at crest; cingulum very irregularly sinuous in lingual view; posterior of lingual basin occasionally with well defined tubercle. Base of crown tumid.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in occlusal view; very slightly constricted across median valley; lophs low, slightly bowed anteriorly; metaloph broader than protoloph in M^1 and M^2, approximately equal in M^3 and somewhat narrower in M^4. Anterior cingulum low, broad, short, nearly planar transversely; generally no trace of distinct forelink present, but low, weak ridge occasionally passes from base of protoloph to cingulum, near crown axis; anteriorly, cingulum flattened or broadly curved; relatively strong ridge ascends from paracone, uniting with labial margin of cingulum, strongly delimiting labial extremity of cingular shelf; slight anterolingual fossette usually present at lingual extremity of anterior cingular shelf. Midlink relatively strong, moderately low, curving only very slightly posterolabially from protocone to unite with slight ridge from near midpoint of metaloph, above median valley; strong ridge ascends posteriorly from paracone, then curves lingually to cross median valley about one-half way between midlink and labial margin; ridge usually unites with very weak ridge ascending anterolingually from metacone; labial moiety of median valley sharply U-shaped; lingual limit of valley occasionally tuberculate, but usually smooth. Strong slightly flared ridge ascends posterolingually from hypocone to above metacone, uniting with lesser ridge ascending from metacone; posterior fossette well defined, shallow, delimited by ridges from posterior cusps slightly labiad to crown axis.

DISCUSSION: *Protemnodon devisi* sp. nov. is the best represented protemnodont in the Chinchilla fauna. The bulk of the material here referred to *P. devisi*, like that of *P. chinchillaensis* described above, was originally referred by De Vis (1895) to *P. anak*. The species is known only from fragmentary mandibular and maxillary remains and, while no associated cranial remains have been recovered, the maxillae are referred on the basis of both size and morphology.

Table 15 presents summaries of mandibular and maxillary measurements for *P. devisi*, while Table 16 indicates measurements for the holotype, F4710. Variation, as expressed by the Coefficient of Variation, is consistent with that in other species of *Protemnodon*. Generally, the sample is reasonably adequate for mandibular remains but is too small for all but general conclusions on the maxillary characters considered. Morphological variation in the premolar teeth is illustrated in Figure 8.

Plane (1972) considers the possibility that this Chinchilla species may represent a local population of *P. otibandus* Plane, described from the Awe fauna in the Middle Pliocene Otibanda Formation, Bulolo, Papua and New Guinea and recorded by Plane (1972) in the marine Lower Pliocene (Kalimnan) Jemmy's Point Formation, Victoria. At present, however, sufficient morphological distinctions are present in the Chinchilla sample, here referred to *P. devisi*, to justify its description as a distinct species, and the Jemmy's Point specimen could equally well relate to this material.

In particular, *P. devisi* is distinguished from *P. otibandus* by its smaller permanent premolars and generally larger molars. The trigonid basin in lower molars is broader in *P. devisi* while the anterior cingulum in upper molars also appears broader. The upper molars are less ovate in occlusal view, and usually have a moderately well defined lingual swelling at the margin of the median valley. The distinct cuspid at the labial end of the talonid basin in M_1, regarded by Plane (1967) as diagnostic in *P. otibandus*, is not developed in any specimen of *P. devisi*. While no attempt has been made to define post-cranial elements in *P. devisi*, adequate material referable to the genus exists in the Chinchilla Sand collections to ensure representation of both this species and *P. chinchillaensis*. Sufficient differences exist in this material, particularly in the bones of the feet, to suggest that the distinctions outlined for cranial remains are apparently reflected in other skeletal elements.

Compared with *P. chinchillaensis*, *P. devisi* is larger in many of its molar dimensions but it has smaller premolars. Morphologically, *P. devisi* has a more robust ramus, a more elevated symphysis, and lacks the swollen bases to the protolophids so evident in *P. chinchillaensis*. As with all Pliocene species yet described, *P. devisi* has lower crowned teeth than Pleistocene species.

It is evident by comparison with the summary of measurements presented for *P. brehus* (Table 6) that overlap occurs. However, apart from the lower crown heights in *P. devisi*, the species are chiefly distinguished by the generally shallower ramus in the Pliocene form, the lower, less curved links in upper and lower molars and the more labiad positioning of these in the lower molars. Compared with *P. roechus*, overlap occurs in many of the characters assessed statistically. Morphologically, the species are separated by many features including the greater elevation of the symphysis and shallower depth of the ramus in *P. devisi*, its lower crowned teeth, its more complex premolar

accessory ridge structure, and the well developed posterior cingulum present in its lower molars. *P. anak* is somewhat smaller than *P. devisi* but again overlap occurs in dental dimensions considered. The species are separated by use of a number of characters including the more elevated nature of the symphysis in *P. devisi*, the lower crown heights present in the Pliocene species, the broader anterior cingulum in its lower molars and the strong accessory ridging in its upper molars.

In addition to the material referred to *P. devisi* from the Chinchilla Sand, the only other specimen from a locality other than this is AM F15464, a left mandibular ramus with M_2–M_4, from a well at 125 feet depth, six miles from Mullaley near Coonabarabran, New South Wales. Measurements for this specimen are presented in Table 16.

DISCUSSION

At present, five species of *Protemnodon* Owen are known from the Upper Cainozoic deposits of Queensland, these comprising *P. anak, P. brehus, P. roechus* from the Pleistocene fluviatile deposits and *P. chinchillaensis* and *P. devisi* from the Late Pliocene Chinchilla Sand. A sixth species, *P. otibandus,* has been recorded from the Lower Pliocene of Victoria. It would appear that the Pleistocene species were widespread throughout Australia, but in many instances critical evaluation of collections made from sites other than in the east coast area will be required before distribution of the species can be more conclusively defined. Of the Pliocene species, *P. chinchillaensis* is restricted to the Chinchilla Sand but *P. devisi* is also recorded from near Mullaley, New South Wales. The specimen referred by Plane (1972) to *P. otibandus* could also relate to this species.

Figure 9 illustrates data derived from the Queensland samples of *Protemnodon* in the form of a log difference diagram (Simpson, 1941). This shows comparatively the proportional relationships of some dental parameters, based on *P. anak* as a standard. It is apparent that *P. brehus* and *P. roechus* are very similar to one another but differ considerably from *P. anak*. In particular the teeth in the larger Pleistocene species are relatively broader than corresponding teeth in *P. anak*. The Chinchilla Sand species have teeth which compare closer in relative proportions with *P. brehus* and *P. roechus* than with *P. anak*. Exceptions to this lie mainly in the permanent premolars in *P. chinchillaensis* which are relatively more elongate than in any other species represented and in the lower heights of the molar teeth in the Late Pliocene species. This latter feature is consistently observed in all known Pliocene species and increase in height of crown would appear to represent one of the Upper Cainozoic evolutionary trends.

The origins of *Protemnodon* are obscure although Stirton *et al.* (1967b) record the presence of a protemnodont in the Late Oligocene or Early Miocene Wipijiri Formation, Tirari Desert, while Woodburne (1967) records a possible protemnodont in the Late Miocene or Early Pliocene Alcoota fauna from the Waite Formation in central Australia. The species *Hadronomas puckridgei* Woodburne, also described from the Alcoota fauna and suggested by Woodburne (1967) as being close to the lineage leading to the Sthenurinae, could equally well be considered near the lineage leading to the Upper Cainozoic protemnodonts (Bartholomai, 1972a). Within the group it appears likely that

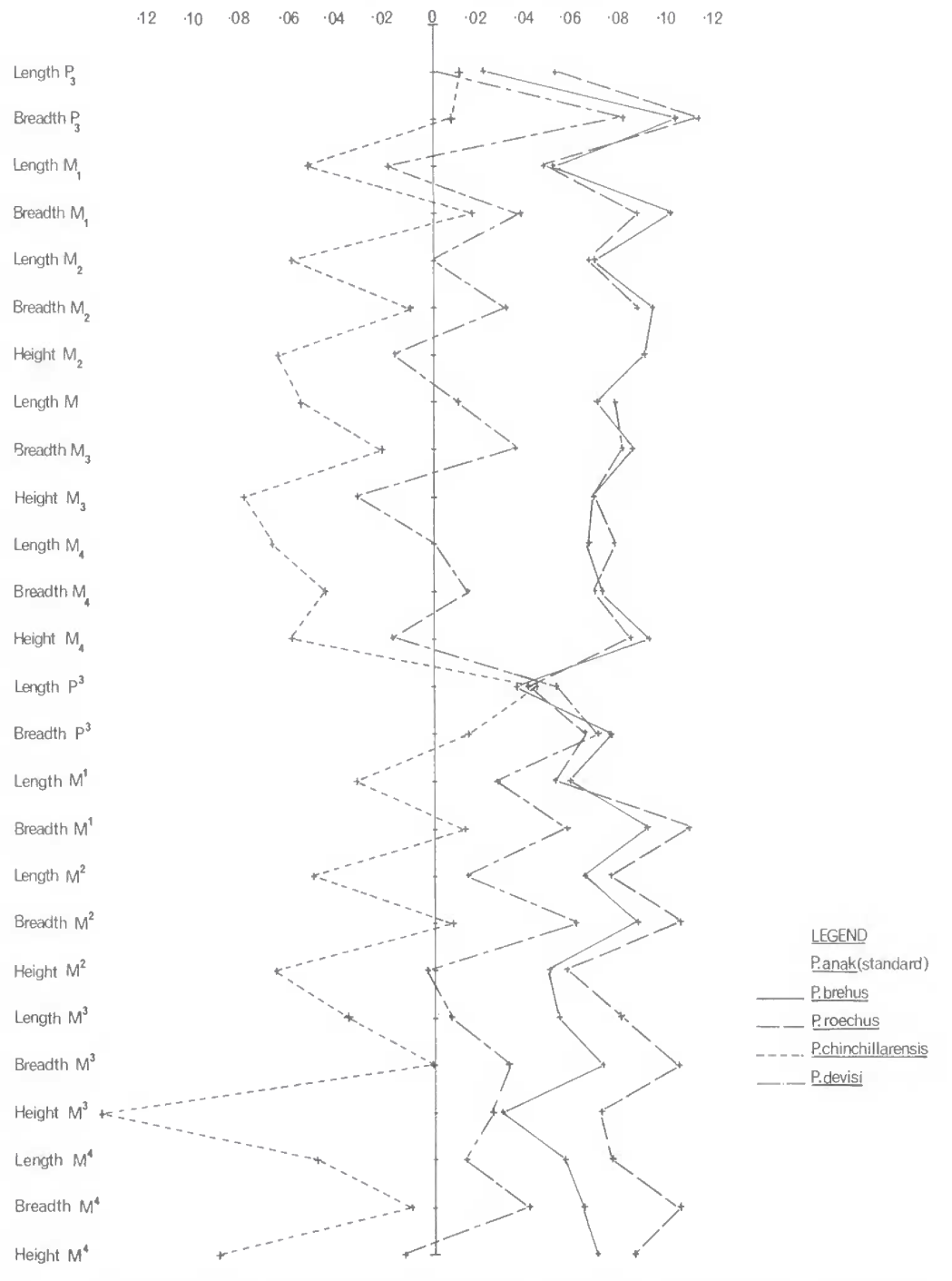

FIG. 9: Log Difference Diagram indicating the proportional relationships of mean values of samples of lower and upper permanent cheek teeth in *Protemnodon* spp., utilizing data for the mean of *P. anak* as standard. Mean values for each species have been connected to facilitate comparison.

P. devisi is closely related to *P. otibandus* on the one hand and to *P. brehus* and *P. roechus* on the other. *P. chinchillaensis* may relate with *P. anak* in the Pleistocene but morphological support for this is not as strong as for the relationships of *P. devisi*.

It is obvious from what is known of the morphology of *Protemnodon* that the genus was adapted primarily as a grazing animal and its relative abundance in the Pleistocene fluviatile deposits of the Darling Downs area is in keeping with the proposals that the region during that time comprised well watered, open sclerophyll and open grassland areas ideally suited to grazing and browsing macropodids. Similar palaeoecological conditions are proposed for the Late Pliocene situation in the western Darling Downs area.

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PLATE 9

Protemnodon anak Owen, 1874

FIG. 1: Lateral view of incomplete cranium, F616, eastern Darling Downs, × ½.
FIG. 2: Occlusal view of F616, × ½.
FIG. 3: Lateral view of partial right premaxilla, F3672, showing vestigeal C^1, Ravensthorpe, Pilton, Darling Downs, × 1.
FIG. 4: Lateral view of partial premaxillae, F651, Gowrie, eastern Darling Downs, × 1.
FIG. 5: Occlusal view of F651, × 1.

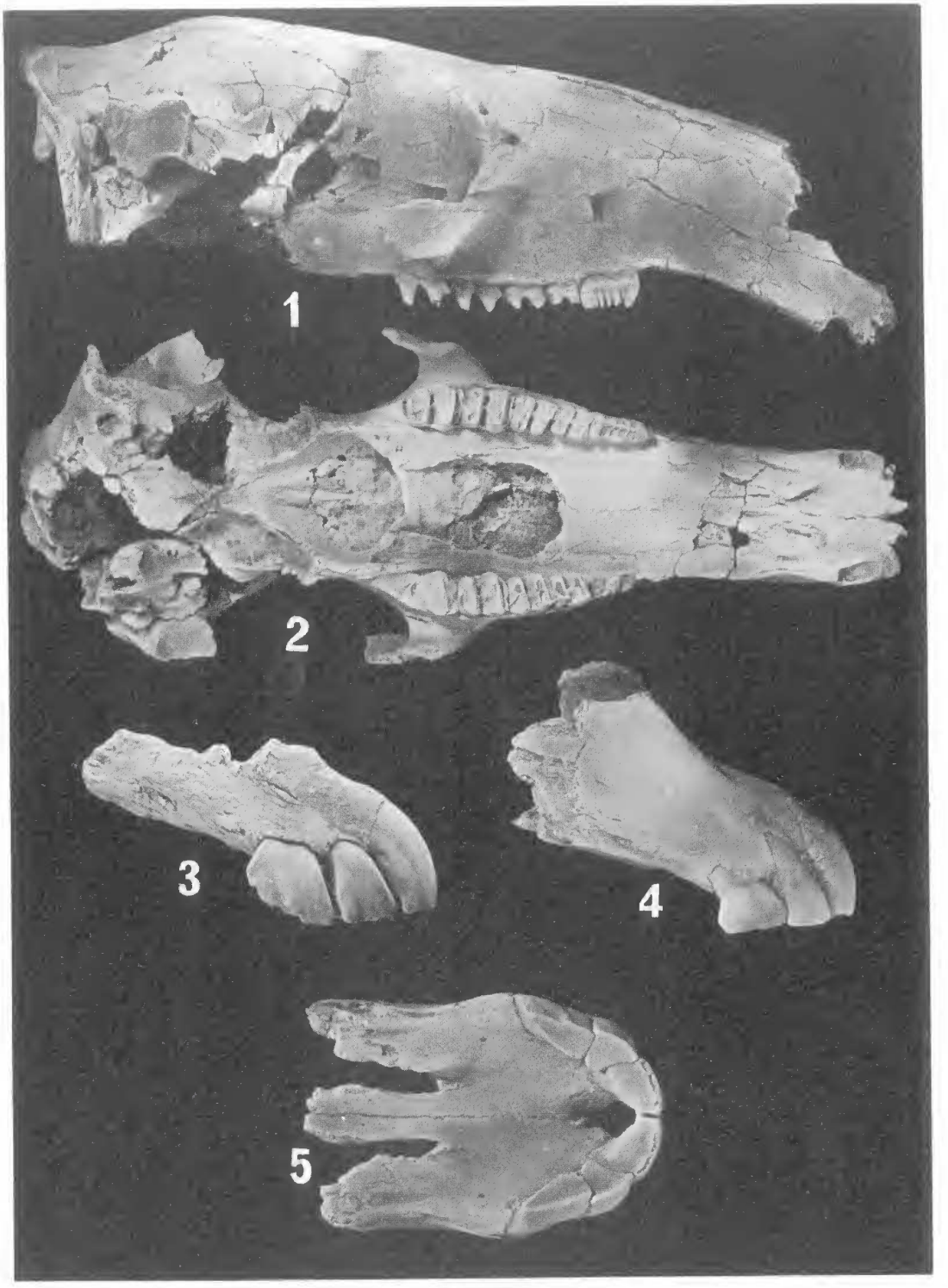
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PLATE 10

Protemnodon anak Owen, 1874

FIG. 1: Lateral view of incomplete juvenile maxilla, F3677, eastern Darling Downs, × 1.

FIG. 2: Stereopair of occlusal view of F3677, × 1.

FIG. 3: Lateral view of incomplete adult maxilla, F4896, Gowrie, Darling Downs, × 1.

FIG. 4: Stereopair of occlusal view of F4896, × 1.

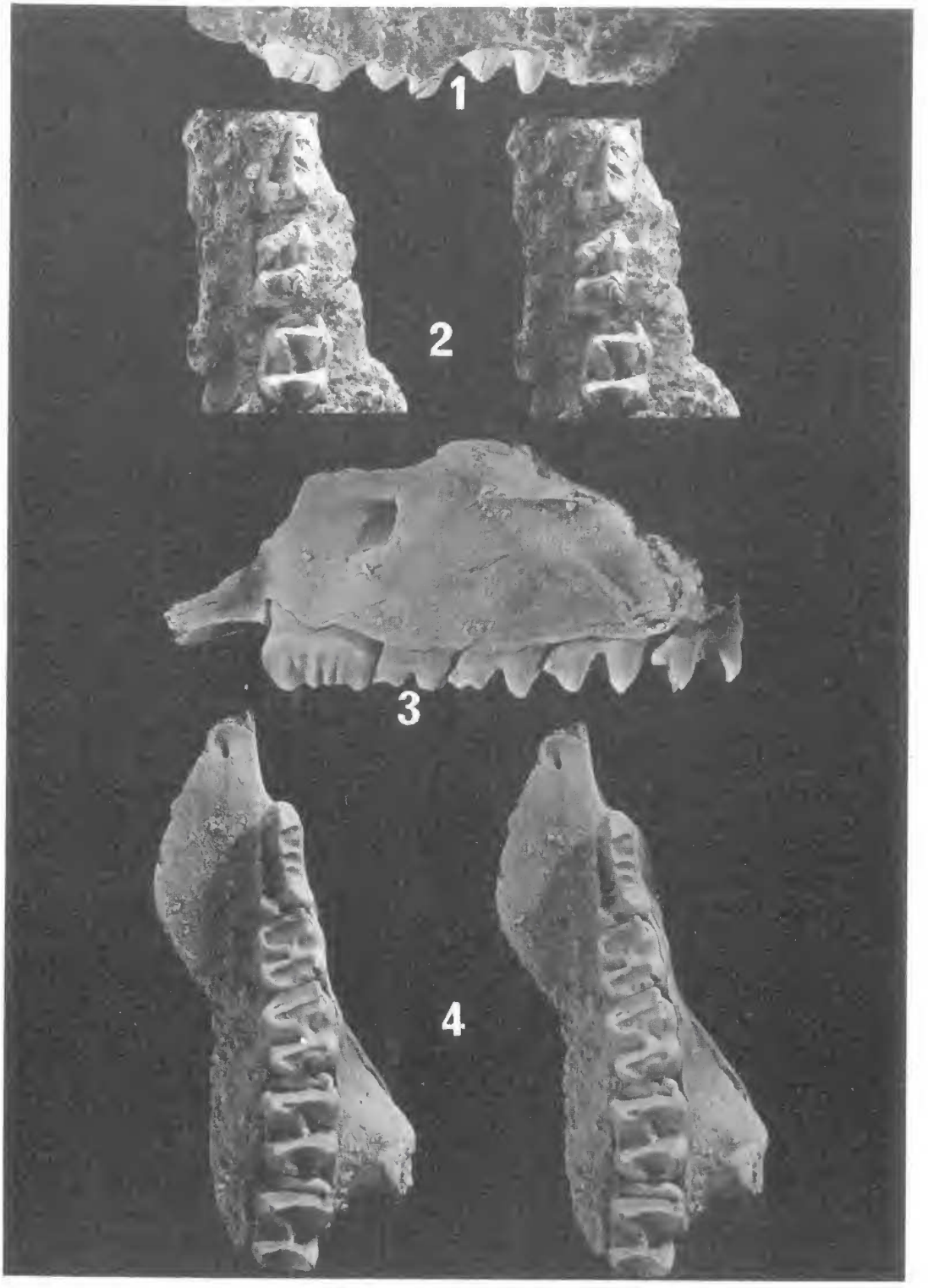
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PLATE 11

Protemnodon anak Owen, 1874

FIG. 1: Stereopair of occlusal view of juvenile mandibular rami, F3051, Gowrie, Darling Downs, × 1.

FIG. 2: Lateral view of F3051, × 1.

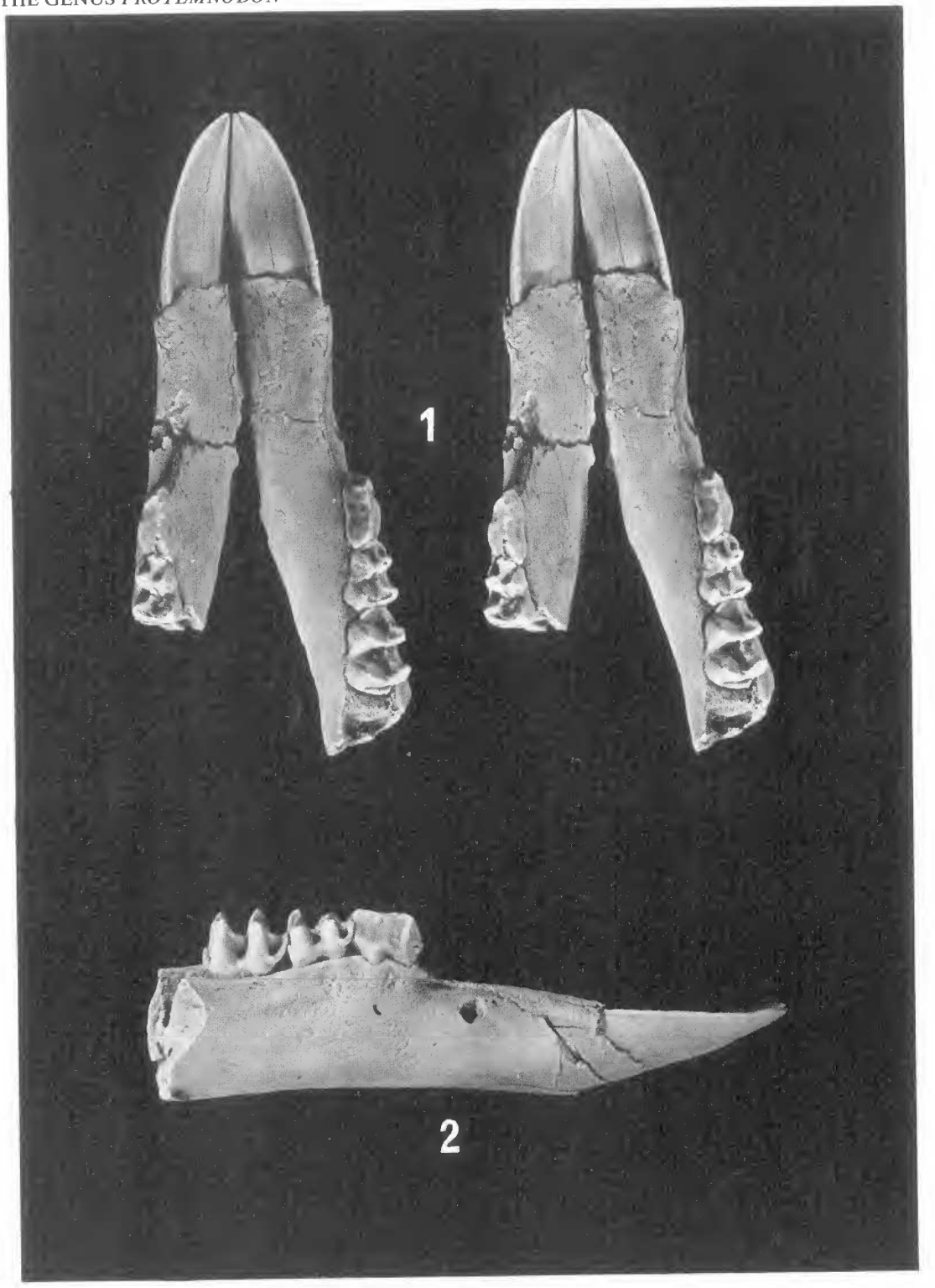
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PLATE 12

Protemnodon anak Owen, 1874

FIG. 1: Lateral view of adult mandible, F3034, eastern Darling Downs. × 1.

FIG. 2: Stereopair of occlusal view of F3034, × 1.

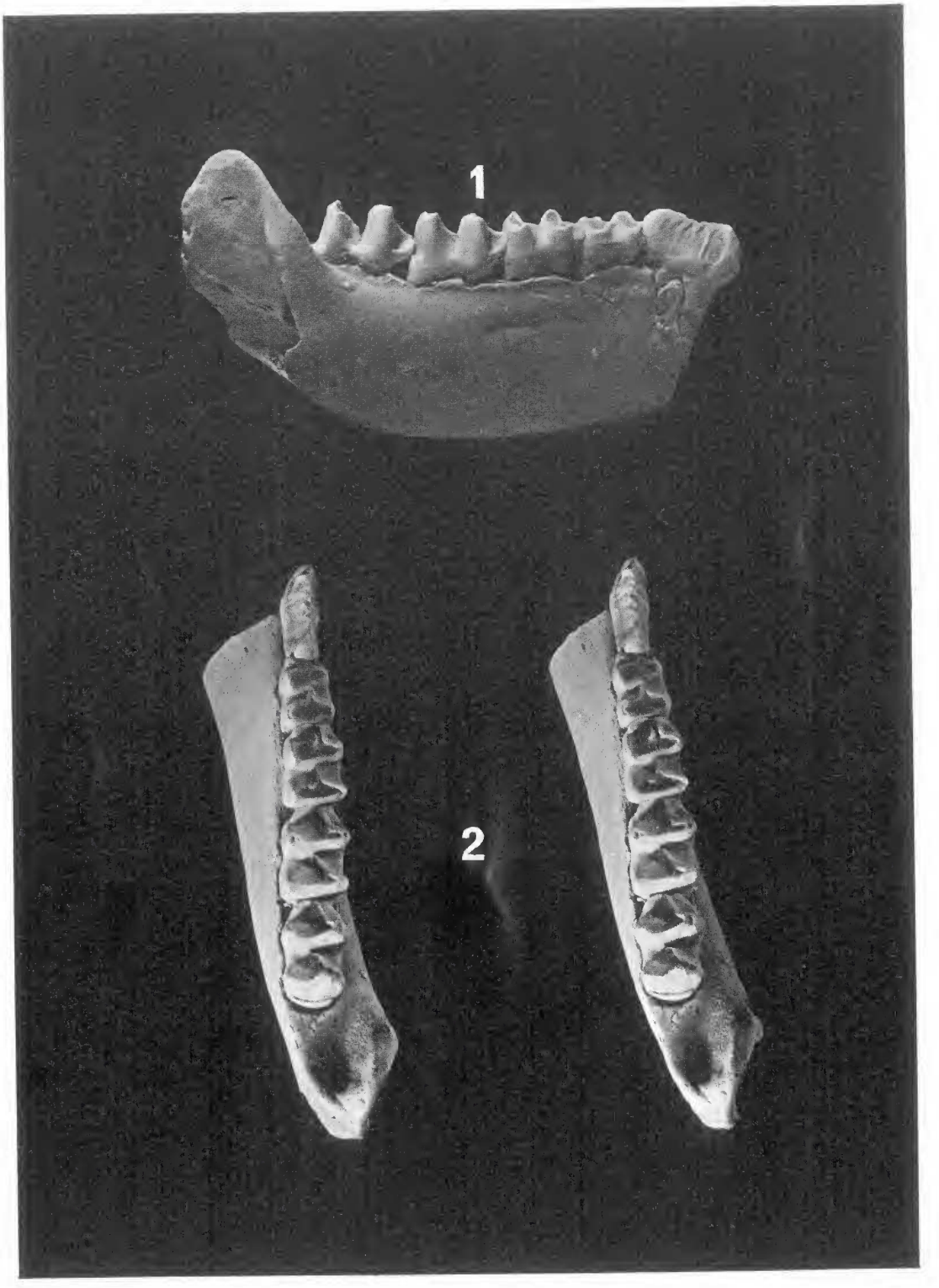
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PLATE 13

Protemnodon brehus (Owen, 1874)

FIG. 1: Lateral view of adult maxilla, F4947, eastern Darling Downs, × 1.

FIG. 2: Stereopair of occlusal view of F4947, × 1.

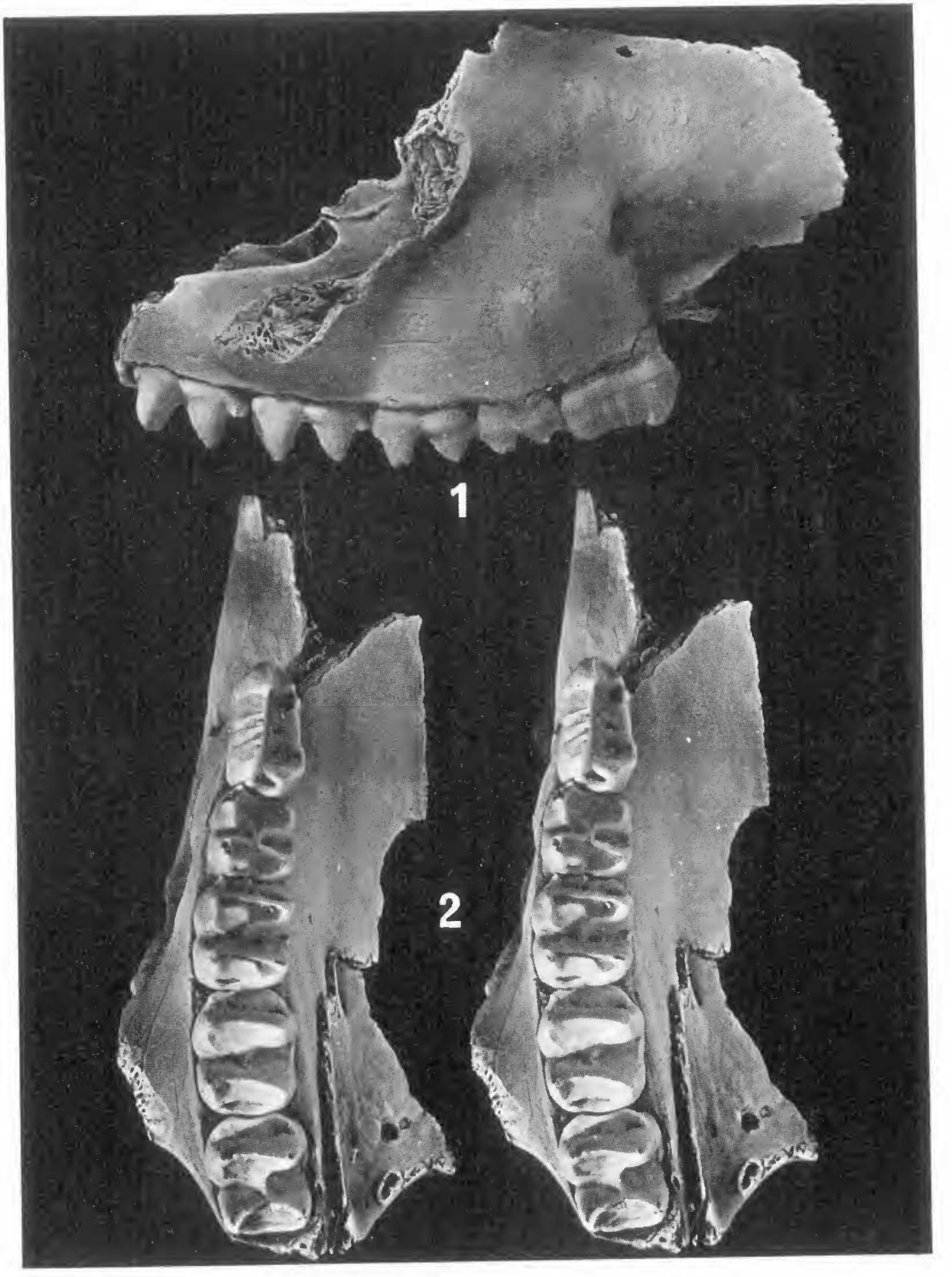
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PLATE 14

Protemnodon brehus (Owen, 1874)

FIG. 1: Lateral view of juvenile mandible, F3027, eastern Darling Downs, × 1.

FIG. 2: Stereopair of occlusal view of F3027, × 1.

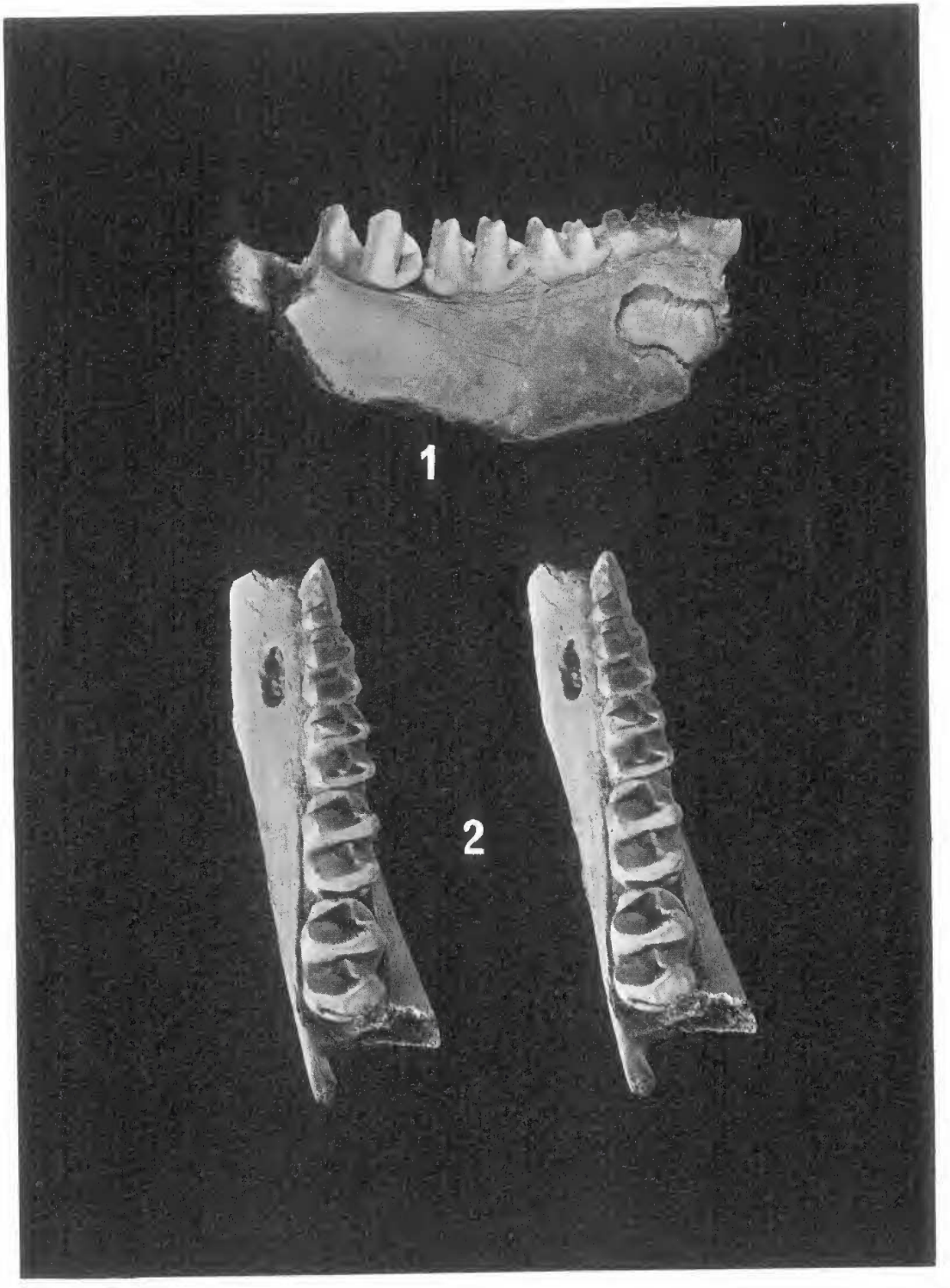
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PLATE 15

Protemnodon brehus (Owen, 1874)

FIG. 1: Lateral view of adult mandible, F3029, eastern Darling Downs, × 1.

FIG. 2: Stereopair of occlusal view of F3029, × 1.

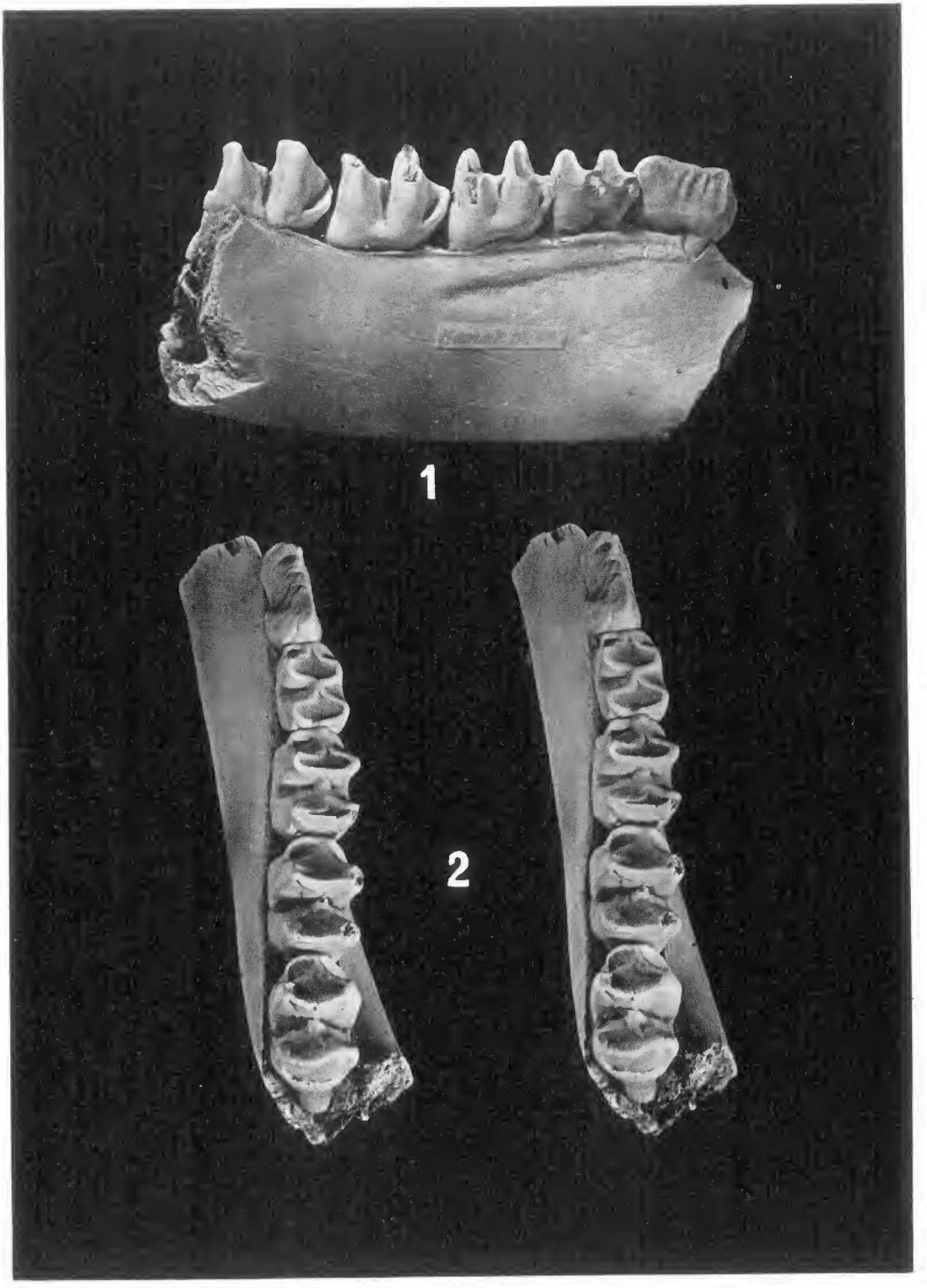
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PLATE 16
Protemnodon roechus Owen, 1874

FIG. 1: Labial view of partial premaxilla, F5053, eastern Darling Downs, × 1.
FIG. 2: Stereopair of occlusal view of F5053, × 1.

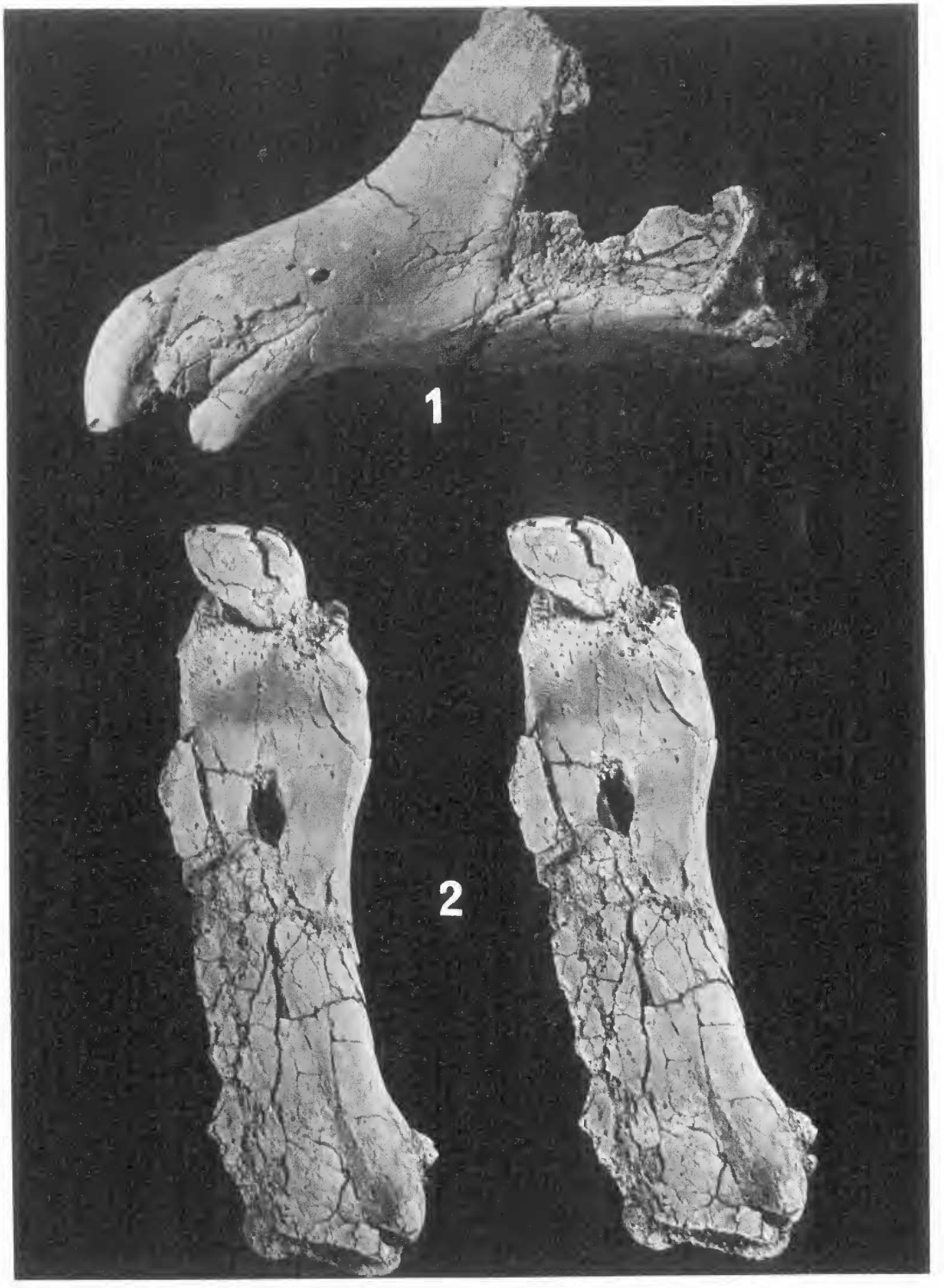
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PLATE 17

Protemnodon roechus Owen, 1874

FIG. 1: Labial view of adult maxilla, F4948, eastern Darling Downs, ×1.

FIG. 2: Stereopair of occlusal view of F4948, ×1.

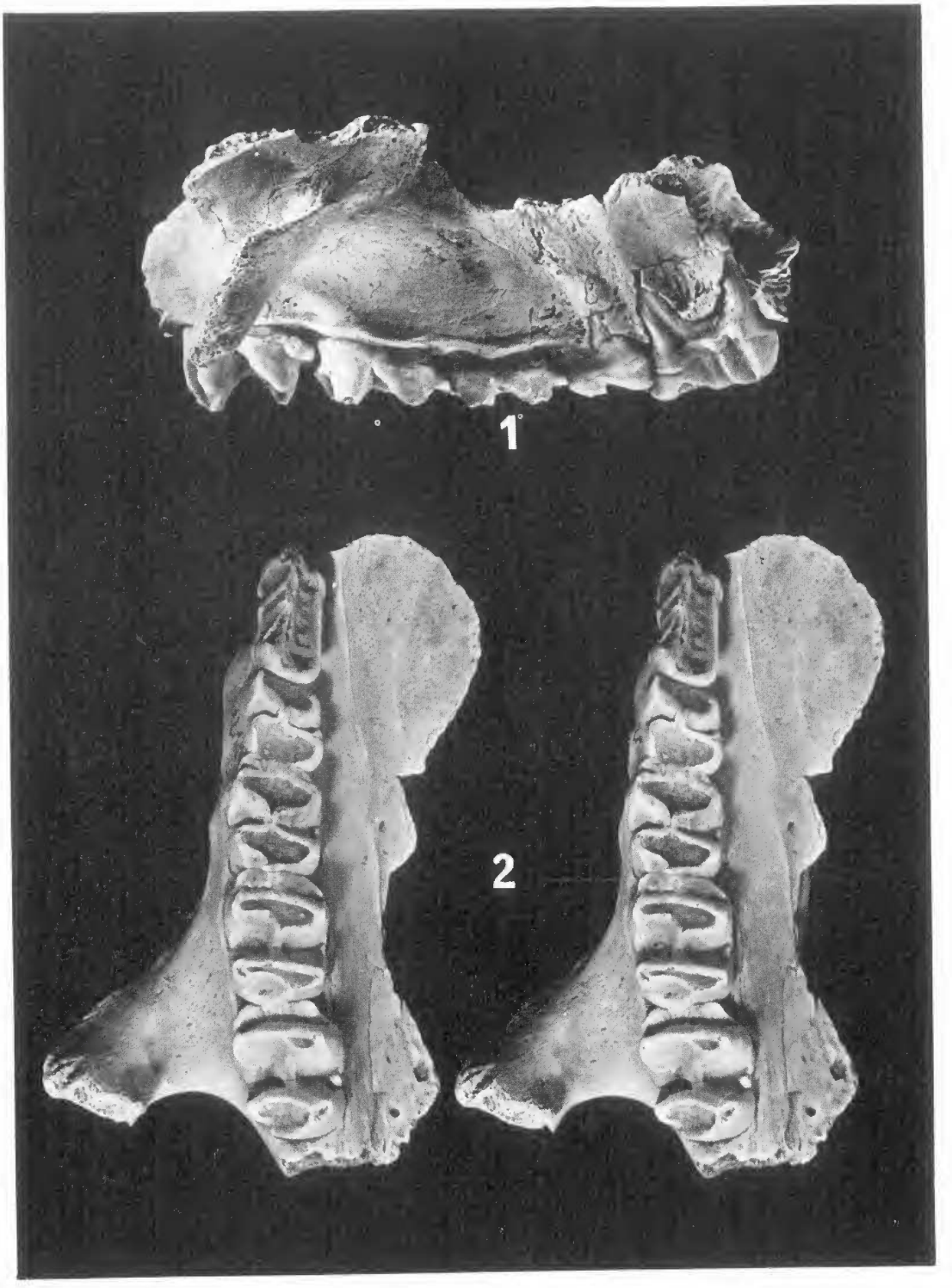
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PLATE 18

Protemnodon roechus Owen, 1874

FIGS. 1, 1a: Occlusal view of partial associated juvenile mandibular rami with stereopair of right mandible, F647, eastern Darling Downs, × 1.

FIG. 2: Lateral view of F647, × 1.

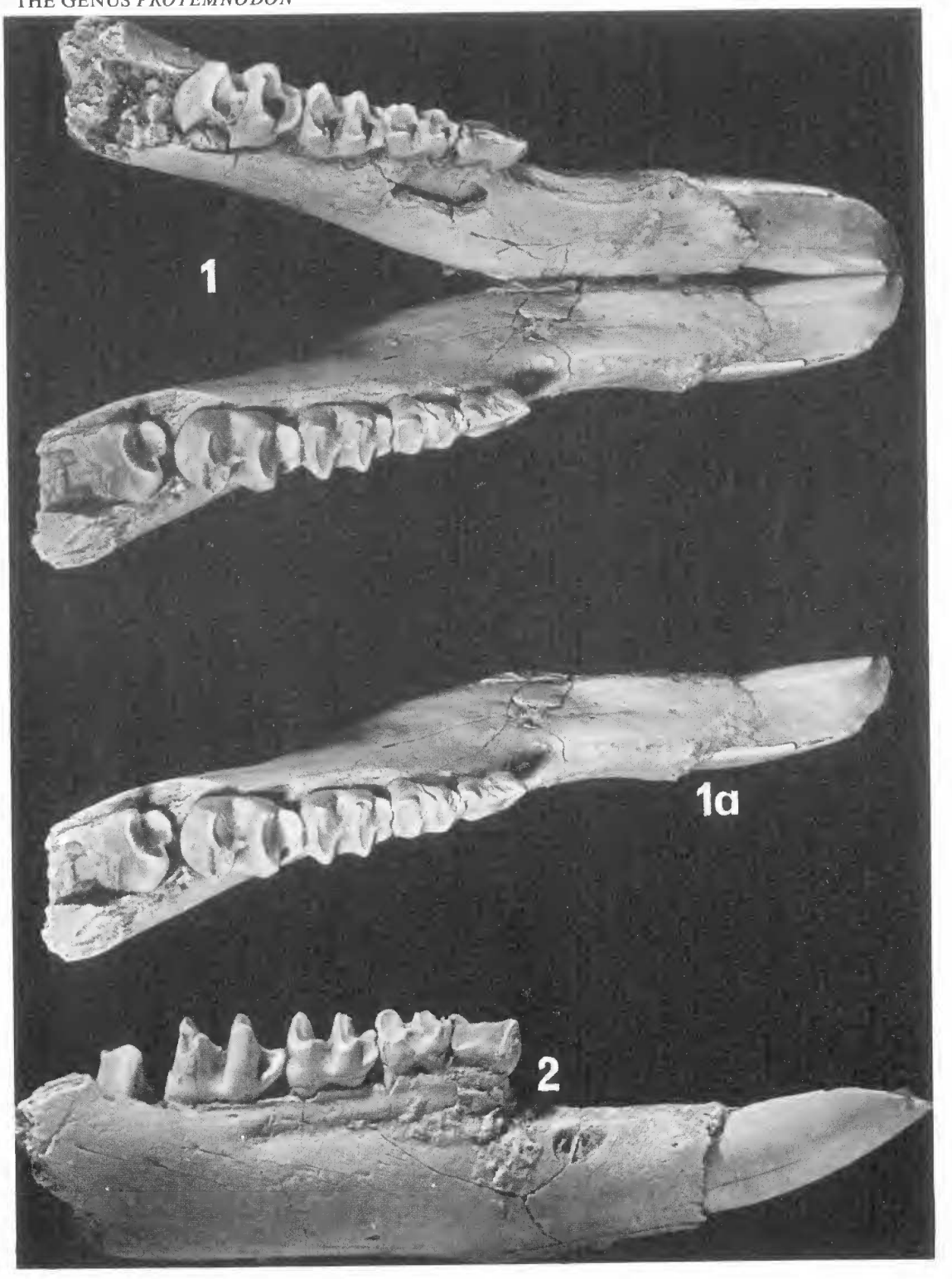
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PLATE 19

Protemnodon roechus Owen, 1874

FIG. 1: Labial view of partial adult mandible, F3033, eastern Darling Downs, ×1.

FIG. 2: Stereopair of occlusal view of F3033, ×1.

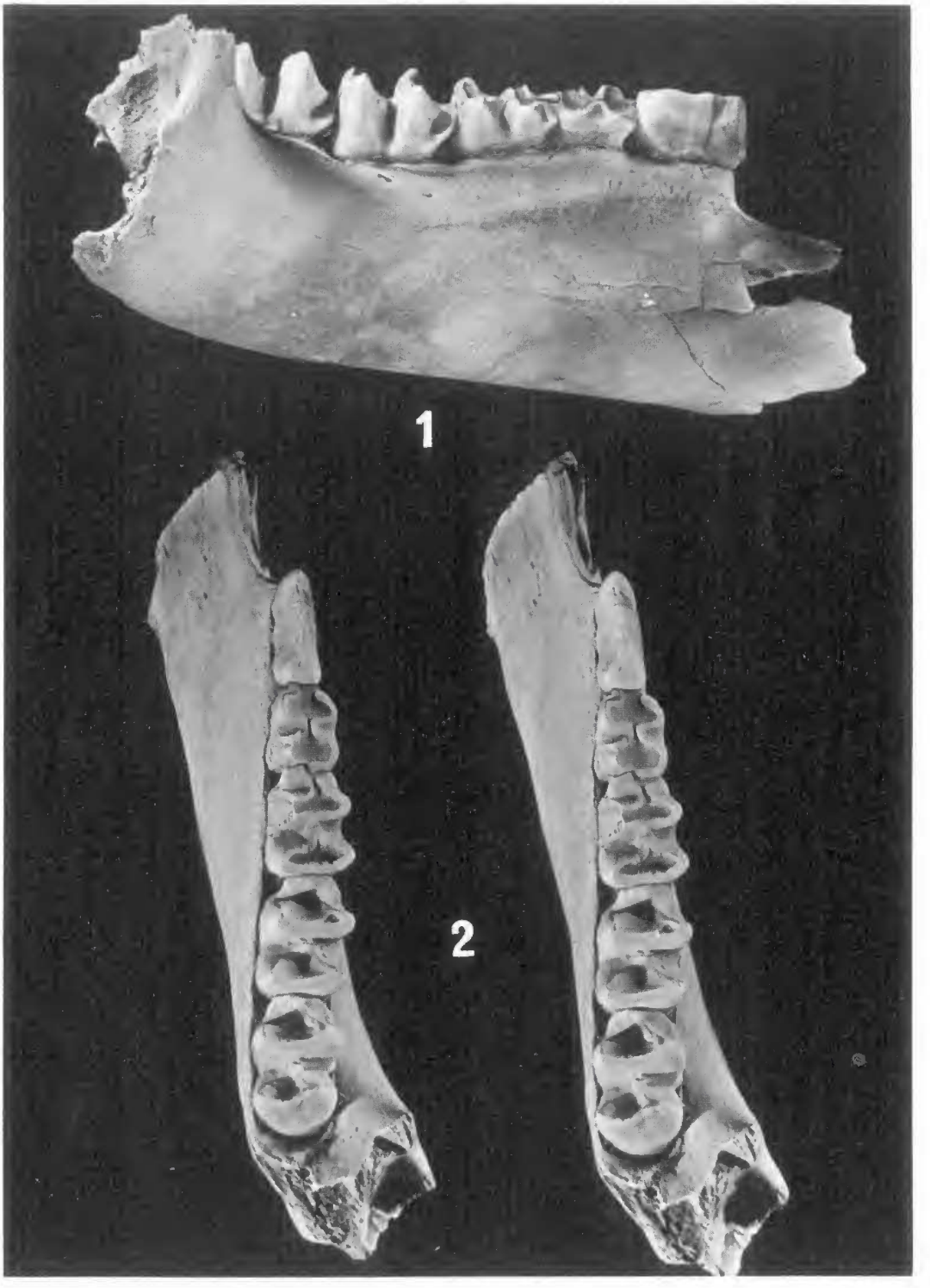
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PLATE 20

Protemnodon chinchillaensis sp. nov.

FIG. 1: Lateral view of partial juvenile maxilla, F5239, western Darling Downs, × 1.
FIG. 2: Stereopair of occlusal view of F5239, × 1.
FIG. 3: Lateral view of partial adult maxilla, F4719, Chinchilla, Darling Downs, × 1.
FIG. 4: Stereopair of occlusal view of F4719, × 1.

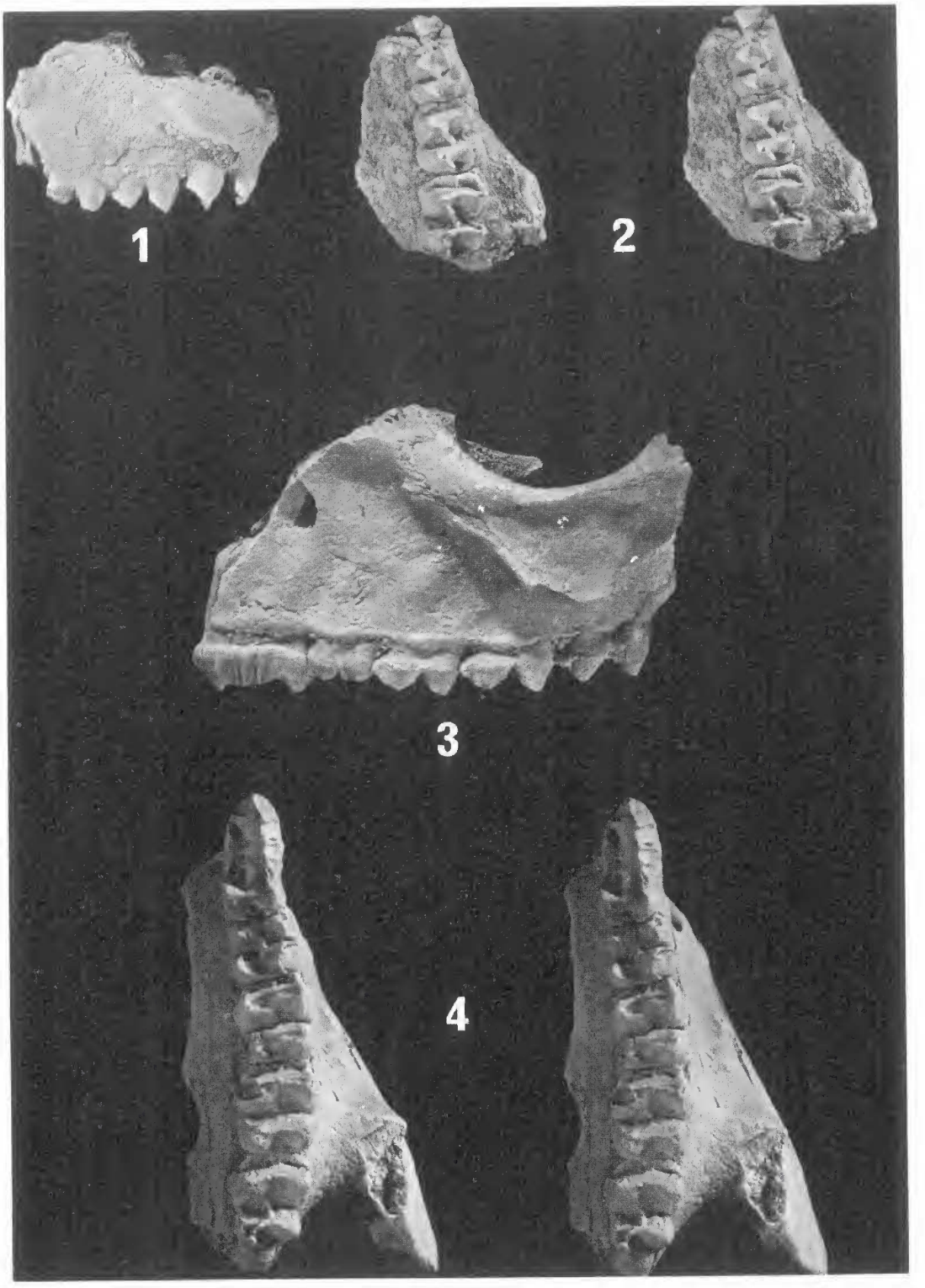
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PLATE 21

Protemnodon chinchillaensis sp. nov.

FIG. 1: Lateral view of partial juvenile mandible, F5242, Chinchilla, Darling Downs, × 1.
FIG. 2: Stereopair of occlusal view of F5242, × 1.
FIG. 3: Lateral view of holotype, partial adult mandible, F5246, Chinchilla, Darling Downs, × 1.
FIG. 4: Stereopair of occlusal view of holotype, F5246, × 1.

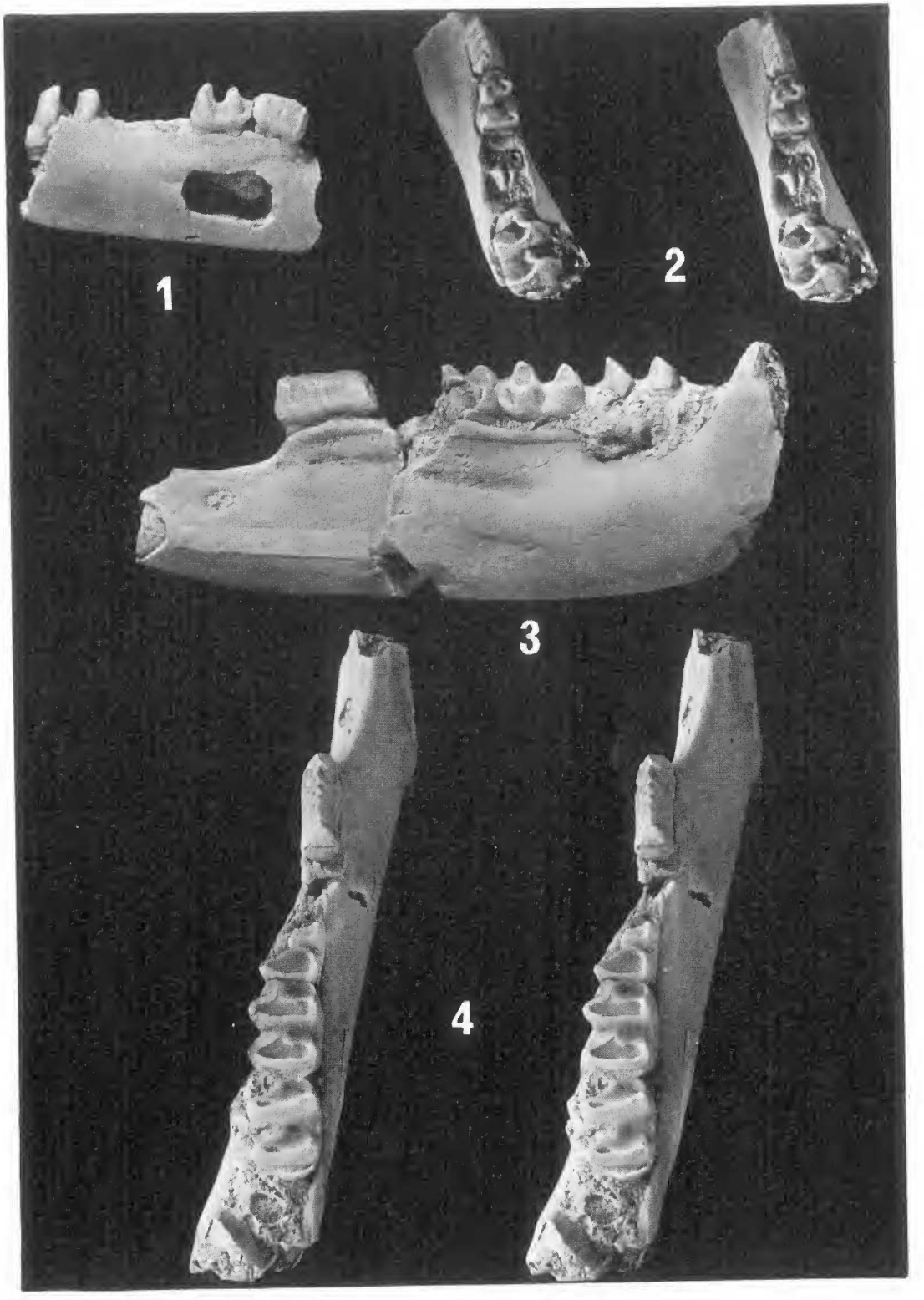
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PLATE 22

Protemnodon devisi sp. nov.

FIG. 1: Lateral view of partial adult maxilla, F4688, western Darling Downs, × 1.
FIG. 2: Stereopair of occlusal view of F4688, × 1.
FIG. 3: Lateral view of partial juvenile maxilla, F4712, Chinchilla, Darling Downs, × 1.
FIG. 4: Stereopair of occlusal view of F4712, × 1.

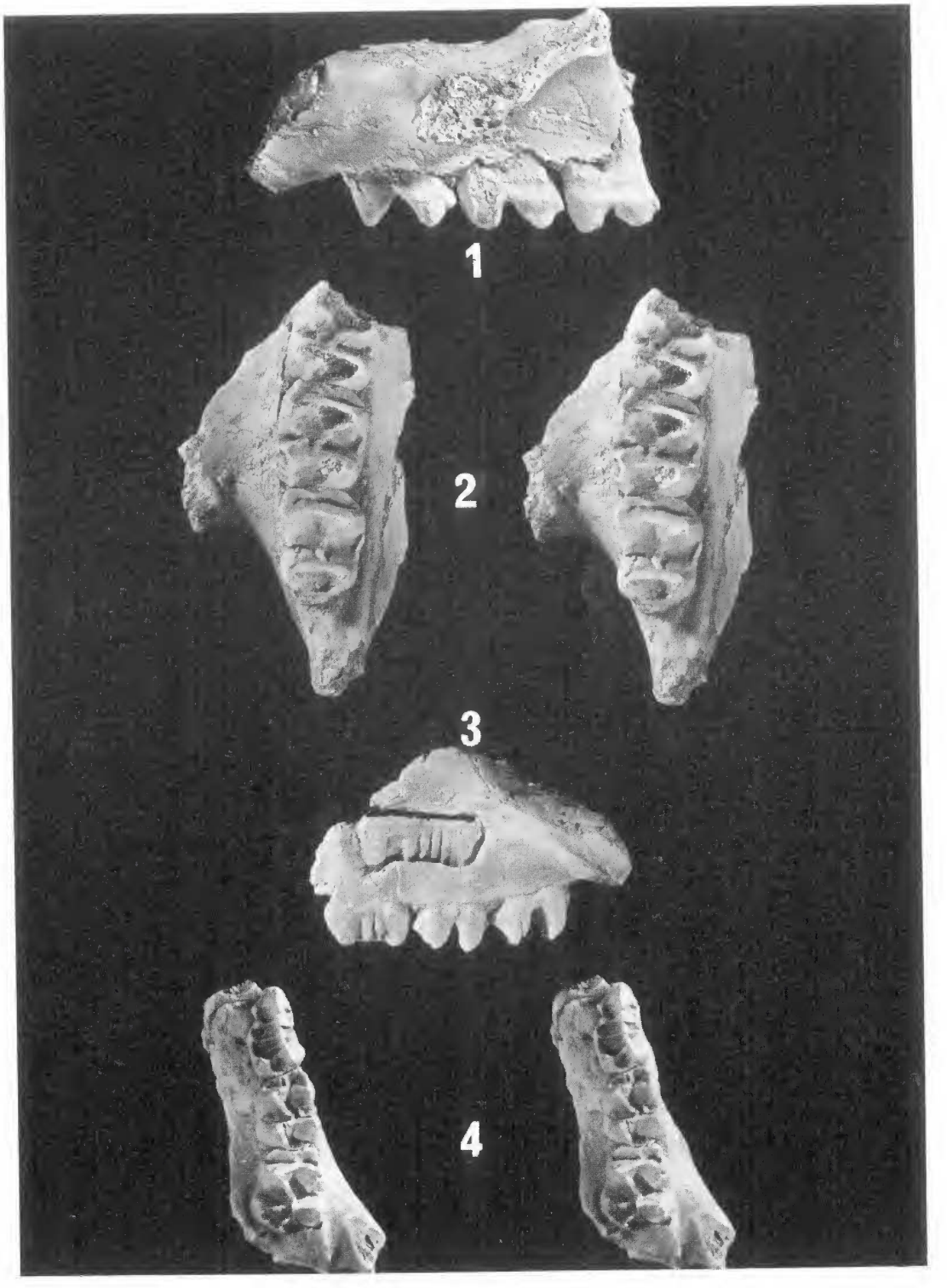
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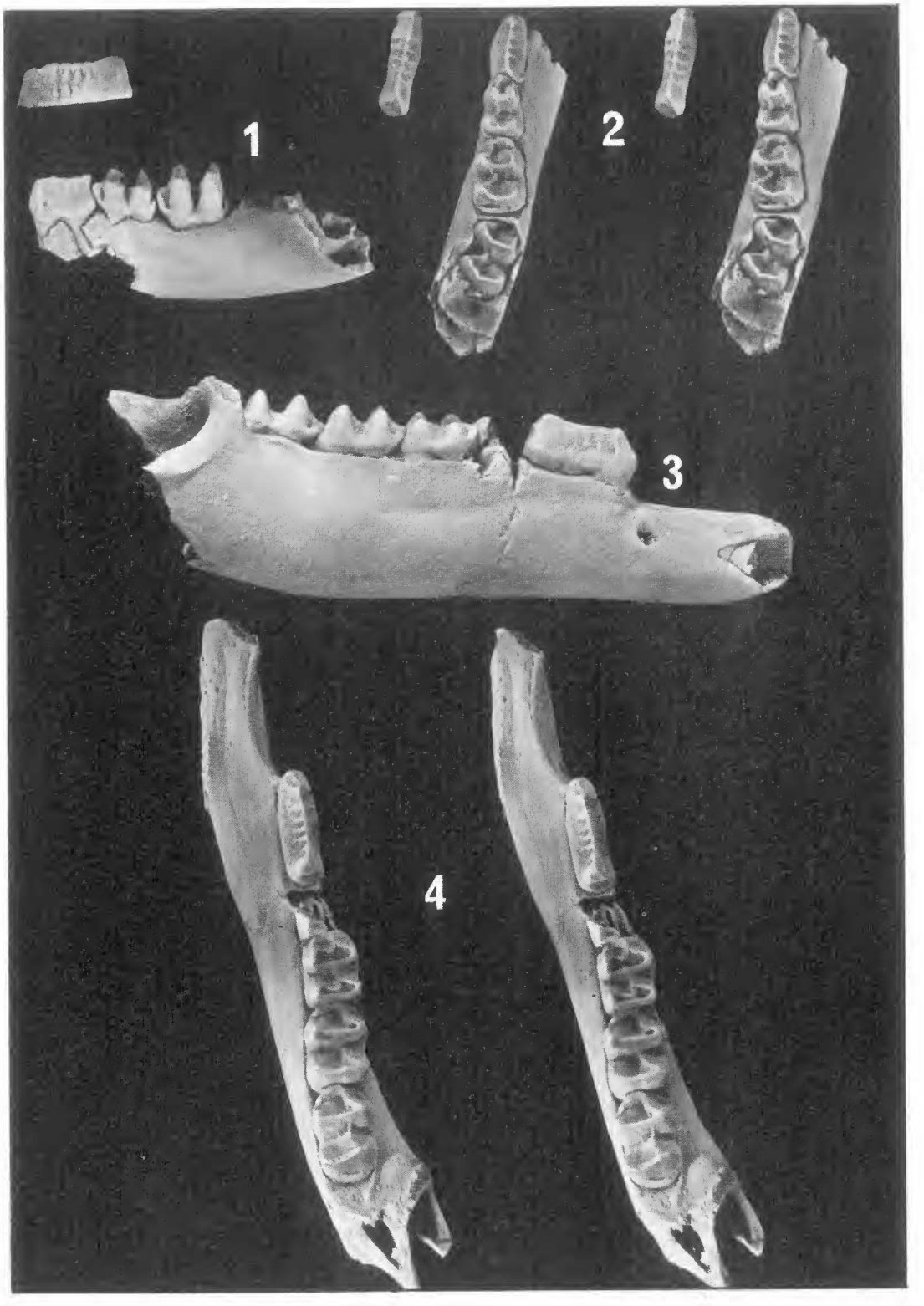
PLATE 23

Protemnodon devisi sp. nov.

FIG. 1: Lateral view of partial juvenile mandible with excavated P_3, F4797, western Darling Downs, × 1.
FIG. 2: Stereopair of occlusal view of F4797, × 1.
FIG. 3: Lateral view of holotype, partial adult mandible, F4710, Chinchilla, Darling Downs, × 1.
FIG. 4: Stereopair of occlusal view of holotype, F4710, × 1.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